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The Case for Chiropteran Monophyly

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ABSTRACT

The current controversy concerning bat monophyly centers on relationships of Microchiroptera, Megachiroptera, Primates, and several other groups of mammals. Despite claims to the contrary, studies of both molecular and morphological data strongly support bat monophyly and a single origin for powered flight in mammals. Analyses of some molecular data sets have yielded inconclusive results (e.g., rDNA restriction sites, αA-crystallin amino acid sequences, and cytochrome oxidase subunit I gene nucleotide sequences). However, analyses of most biochemical and molecular data support monophyly of bats (e.g., albumin immunological distances, DNA-DNA hybridization, α-globin + β-globin amino acid sequences, nucleotide sequence data from the ε-globin gene, interphotoreceptor retinoid binding protein gene, 12S rRNA gene, and cytochrome oxidase subunit II gene). In no instance have molecular data provided unambiguous support for bat diphyly. Morphological data show a slightly different pattern. Neural and penial characters support diphyly of bats, but other data subsets clearly support bat monophyly (e.g., characters of the cranium and postcranial skeleton, vascular system, muscles, and fetal membranes). When all of the morphological data are considered together, the combined data set strongly supports bat monophyly. Over 25 morphological synapomorphies—many of which consist of complex suites of modifications—diagnose the monophyletic order Chiroptera. The fact that these synapomorphies represent many different anatomical systems further strengthens the case for chiropteran monophyly.

INTRODUCTION

Monophyly of Chiroptera—and a single origin for powered flight in mammals—has been assumed by most evolutionary biologists because all bats apparently share a unique set of specializations for flight. However, bat monophyly and homology of the chiropteran wing have been questioned by authors who have suggested that Megachiroptera and Microchiroptera may not be sister taxa (Jones and Genoways, 1970; Smith, 1976, 1980; Smith and Madkour, 1980; Hill and Smith, 1984; Pettigrew, 1986, 1991a, 1991b; Pettigrew and Jamieson, 1987; Pettigrew et al., 1989). If the two major bat lineages are only distantly related and their most recent common ancestor was nonvolant, then a dual origin for wings and powered flight within Mammalia must be hypothesized.

Bat diphyly and related hypotheses (e.g., megachiropterans as "flying primates") have been the focus of intense discussion in recent years, with some authors defending the traditional concept of a monophyletic Chiroptera (e.g., Wible and Novacek, 1988) while others supported bat diphyly (e.g., Pettigrew et al., 1989). In 1991 the controversy was reviewed in a series of papers that appeared together in *Systematic Zoology* (i.e., Baker et al., 1991b; Pettigrew, 1991a, 1991b; Simmons et al., 1991). At that time, much of the relevant data remained unpublished, including several significant molecular studies. As a result, the controversy remained largely unresolved. However, since that time over a dozen new phylogenetic studies have been published (tables 1, 2, 3), and the data supporting different phylogenetic hypotheses have been further critiqued (e.g., Thiele et al., 1991; Johnson and Kirsch, 1993; Kaas and Preuss, 1993; Simmons, 1993). These studies have added considerably to our knowledge and understanding of relevant data and methodological issues, and have set the stage for resolution of the debate.

Microchiroptera and Megachiroptera

In any phylogenetic argument it is important that the taxa under consideration (the "operational taxonomic units") be monophyletic. One aspect of bat systematics that has not been the source of controversy is the status of the two bat suborders—there is general agreement that Megachiroptera and Microchiroptera are each monophyletic taxa (Smith, 1976, 1980; Van Valen, 1979; Novacek, 1980b, 1987; Pettigrew et al., 1989; Pettigrew, 1991a, 1991b; Baker et al., 1991a, 1991b; Kay et al., 1992; Beard, 1993a). Monophyly of Microchiroptera has rarely been questioned because all members of the group share a unique system of laryngeal

echolocation (Fleischer, 1973, 1978; Hill and Smith, 1984; Novacek, 1987; Pettigrew et al., 1989). Many cetaceans also use sophisticated echolocation, but the anatomical basis of the system is quite different (Fleischer, 1973, 1978). In addition to features related to echolocation, all microchiropterans share a unique arrangement of the gray matter in the spinal cord plus several apomorphic features of the cranium and postcranium (Van Valen, 1979; Novacek, 1987; Pettigrew et al., 1989; Kay et al., 1992; Beard, 1993a).

Megachiroptera also appears to be monophyletic. Extant megachiropterans share dental specializations associated with frugivory (Slaughter, 1970; Koopman and MacIntyre, 1980), an unusual bilobed keel on the manubrium (personal obs.), and sperm with several unique structural features (Rouse and Robson, 1986). In addition, the nutrient system of the megachiropteran retina involves a pattern of invasive choroid papillae that is not found in any other vertebrate (Kolmer, 1910, 1911, 1926; Fritsch, 1911; Duke-Endler, 1958; Pedler and Tilley, 1969; Buttery et al., 1990).

A number of well-preserved Eocene fossils provide our earliest record of bat evolution. Several taxa (e.g., *Icaronycteris, Palaeochiropteryx*) once considered to be possible ancestors of all extant bats are now believed to represent early branches of the microchiropteran lineage (Novacek, 1985a, 1987; Habersetzer and Storch, 1987, 1992). Characters supporting placement of these taxa in Microchiroptera include features of the ear, basicranium, dentition, and postcranial skeleton (Novacek, 1985a, 1987). Although many fossils are too fragmentary to assess for most of these characters, dental morphology suggests that virtually all Eocene bats currently known belong to Microchiroptera. One exception is a specimen from the Late Eocene of Thailand, an isolated tooth which appears to be a lower premolar of a megachiropteran bat (Ducrocq et al., 1993).

The best-preserved putative megachiropteran is *Archaeopteropus,* which is known only from a single partial skeleton from the Late Oligocene of Italy (Meschinelli, 1903). The skull and dentition of this specimen are badly damaged, but some evidence suggests that *Archaeopteropus* might have had an insectivorous-type dentition (Revilliod, 1922; Russell and Sigé, 1970; Slaughter, 1970). Nevertheless, *Archaeopteropus* is widely regarded to be a megachiropteran because of similarities in wing morphology shared by this taxon and extant megachiropterans (Anderson, 1912; Revilliod, 1922; Dal Píaz, 1937; Habersetzer and Storch, 1987).

Consideration of the fossil record indicates that the lineages leading to extant megachiropterans and microchiropterans have been separated since at least the Late Eocene, over 50 million years. During this time a great deal of molecular and morphological evolution has taken place, complicating efforts to resolve higher-level relationships (Baker et al., 1991a, 1991b). Many significant morphological, behavioral, and genetic differences exist between Megachiroptera and Microchiroptera (Jones and Genoways, 1970; Pettigrew et al., 1989; Sabeur et al., 1993). Despite these differences, monophyly of bats was more or less assumed between the time Chiroptera was named by Blumenbach (1779) and the early 1970s, when doubts were first raised concerning the evolutionary origins of bats (Gregory, 1910; Simpson, 1945; Jones and Genoways, 1970; Smith, 1980).

Origins of the Bat Monophyly Controversy

Jones and Genoways (1970) were the first to explicitly suggest that Chiroptera might be diphyletic. They discussed the differences between Megachiroptera and Microchiroptera, and pointed out that similarities between these taxa principally involve the flight mechanism. This raised the prospect that "convergent evolution attendant with development of aerial locomotion"—rather than shared ancestry—might account for similarities between megachiropteran and microchiropteran bats (Jones and Genoways, 1970: 5). This idea was further discussed by Smith (1976, 1980), and the first data supporting bat diphyly were presented by Smith and Madkour (1980). Subsequent discussions have focused on relationships of Megachiroptera and Microchiroptera to each other and to other mammalian groups, particularly various "archontan" mammals including Primates, Dermoptera (colugos or gliding le-

murs), Scandentia (tree shrews), and extinct Plesiadapidae and Paromomyidae (fossil forms generally considered related to either primates or dermopterans). With the possible exception of Paromomyidae, all of these taxa appear to be monophyletic (Zeller, 1986; Wible and Covert, 1987; Kay et al., 1992; Beard, 1993a).

Smith and Madkour (1980) identified six derived morphological characters that Megachiroptera shares with archontan taxa other than Microchiroptera, including features of the penis, brain, wrist, and dentition. Inadequate character descriptions and lack of evidence for homology of some derived character states compromised the results of their phylogenetic analysis (see discussion under Results of Morphological Studies), and few systematists accepted Smith and Madkour's (1980) conclusion that bats are diphyletic. Hill and Smith (1984) favored the diphyly hypothesis but presented no new data.

In the late 1980s Pettigrew and his colleagues reported a series of derived features of the nervous system that support chiropteran diphyly. The phylogeny they presented suggests that Megachiroptera is more closely related to Primates and Dermoptera than it is to Microchiroptera, which falls well outside "Archonta" and may represent one of the most basal branches within Eutheria (Pettigrew, 1986, 1991a, 1991b; Pettigrew and Cooper, 1986; Pettigrew and Jamieson, 1987; Pettigrew et al., 1989). Over 20 derived neural traits and one postcranial character have been cited as supporting this hypothesis, although some of these features have yet to be studied in all of the relevant taxa (see summary in Pettigrew, 1991a). Methods of phylogenetic analysis and details of several characters employed by Pettigrew and his colleagues have been questioned by various authors (e.g., Wible and Novacek, 1988; Baker et al., 1991b; Simmons et al., 1991; Thiele et al., 1991; Johnson and Kirsch, 1993; Kaas and Preuss, 1993; Simmons, 1993). However, aspects of the neural data are compelling, and subsequent debate of Pettigrew's conclusions stimulated many morphological and molecular studies (tables 1, 2, 3).

In part as a result of historical development of the controversy, some authors in recent years have treated "bat diphyly" as synonymous with Pettigrew's hypothesis of relationships (i.e., Megachiroptera is more closely related to Primates and Dermoptera than to Microchiroptera). This overlooks the possibility that Megachiroptera might be related to an entirely different set of taxa; Pettigrew and his colleagues might be correct about bat diphyly, yet wrong about the relationships of Megachiroptera and Microchiroptera to other mammals. To avoid confusion between the general concept of bat diphyly and Pettigrew's hypothesis of relationships, the phrase "bat diphyly sensu Pettigrew et al. (1989)" is used in the following discussions to specify the phylogenetic hypothesis supported by Pettigrew and his colleagues.

REVIEW OF PHYLOGENETIC STUDIES

Many different types of molecular and morphological data have been used in studies relevant to the bat monophyly controversy (tables 1, 2). Some studies have focused on data from a single protein, gene, or organ system, while others have attempted to integrate diverse types of data. In general, two categories of data may be recognized: distance data and discrete character data.

Distance data consist of measurements of continuous variables estimated in a series of pairwise comparisons. The "evolutionary distance" separating taxa is calculated at the end of a study by combining data from the comparisons to form a consensus hypothesis. Distance techniques (e.g., immunodiffusion, DNA-DNA hybridization) offer methods for estimating relationships among taxa, but unfortunately provide few means of evaluating the nature of the evidence supporting various relationships. Goodness-of-fit statistics may be employed to evaluate trees, and replications may be performed to calculate confidence limits, but problems exist with underlying assumptions of additivity of distances (Felsenstein, 1984). Distance data do not permit formulation or testing of hypotheses of homology, and patterns of transformation cannot be investigated. Subsets of data from different sources cannot be combined, and it is difficult to compare results of distance analyses with those of discrete character analyses except to note general agreement or disagree-

ment concerning phylogenetic results (i.e., tree topology). Nevertheless, distance techniques provide a valid means for constructing phylogenies (Felsenstein, 1984; Sarich, 1993), and some studies involving distance data are relevant to the issue of bat monophyly.

In contrast to distance techniques, analyses of discrete character data (e.g., morphological traits, amino acid sequences, nucleotide sequences) require formulation and testing of explicit hypotheses of homology. Subsets of data from different sources (e.g., anatomical systems) can be combined in comprehensive analyses or analyzed separately depending on the goals of the study. When phylogenetic analyses have been completed, both tree topology and the evidence supporting various clades (i.e., synapomorphies) can be examined, and results of different studies can be compared. Levels of homoplasy in characters supporting a given clade can be considered when evaluating the strength of the overall evidence supporting a particular phylogenetic conclusion. However, analyses of discrete character data are subject to their own set of problems, including character dependence and problems associated with various weighting schemes. All such issues must be considered when evaluating the results of phylogenetic studies (see discussion in Simmons, 1993).

Taxonomic Sampling

One methodological issue of prime importance in the bat monophyly controversy is taxonomic sampling (Baker et al., 1991b; Simmons, 1993). Both chiropteran suborders present problems because of their enormous diversity. Megachiroptera comprises over 150 extant species referred to a single family, and Microchiroptera includes over 750 extant species referred to 16 families (Koopman, 1993). Because these taxa are speciose, studies of higher-level relationships must settle for sampling only a subset of the species included in each group. This is also true for other relevant taxa including Primates (233 species) and Scandentia (19 species; Groves, 1993; Wilson, 1993).

Not surprisingly, taxonomic sampling has been highly uneven in studies relevant to bat monophyly (tables 1, 2). Some studies have included only one species from each of the bat suborders (e.g., Mindell et al., 1991), while others have examined multiple species representing most or all extant families (e.g., Smith and Madkour, 1980). Sampling of bats in the majority of phylogenetic studies falls somewhere between these extremes (tables 1, 2). Taxonomic sampling of other mammalian orders has similarly varied. Representatives of each of the non-bat archontan orders (Primates, Dermoptera, and Scandentia) are represented in most recent studies because these taxa are central to the bat monophyly controversy. However, sampling within these groups has been uneven, and other orders of mammals considered crucial by some authors (e.g., Insectivora, Carnivora) have been omitted entirely from many phylogenetic analyses (tables 1, 2). Studies relevant to bat monophyly range from those including representatives of only three mammalian orders (e.g., Mindell et al., 1991) to those including representatives of all of the extant orders (e.g., Sarich, 1993).

Taxonomic sampling is often effectively constrained by the type of data under consideration. Among molecular studies, the time and expense involved in nucleotide sequencing have apparently discouraged workers from attempting to sample broadly (table 1), although this is now changing with the increased use of PCR and universal primers. Studies involving amino acid sequence data tend to include a much broader sample of taxa because comparable data for many taxa have been collected over the years in conjunction with different projects (table 1; Czelusniak et al., 1990). Among morphological studies, types of characters that can be observed only with intensive laboratory work (e.g., neural characters, fetal membranes) are generally surveyed in fewer taxa than data which can be easily obtained from standard museum preparations (e.g., craniodental characters). Fossil taxa potentially relevant to the question of bat monophyly (e.g., *Icaronycteris,* paromomyids) can be considered only in the context of morphological data sets that include characters preserved in fossils (e.g., craniodental characters, vascular features associated with osteological features).

Breadth and intensity of taxonomic sampling can affect the results of phylogenetic

studies in several ways, influencing both topology of trees and perceived support for various relationships (Gauthier et al., 1988; Donoghue et al., 1989; Novacek, 1992b, 1994; Simmons, 1993). In studies relevant to bat monophyly, taxonomic sampling does not appear to have had much impact on one central phylogenetic conclusion—virtually all of these studies support monophyly of bats (tables 1, 2). However, different studies have reached different conclusions concerning relationships of Chiroptera to other mammalian orders, results which appear to be due at least in part to sampling effects (see Discussion and Conclusions below). The perceived support for bat monophyly (or any other clade identified in a phylogenetic analysis) depends upon the specific taxa considered and the relative "phylogenetic distance" between the groups included in the study. Poor sampling within bats may falsely indicate that some variable characters are fixed synapomorphies of Chiroptera, or may suggest that characters are ambiguous when they in fact are not. Poor sampling of other mammalian orders may have similar effects, and support for chiropteran monophyly may be over- or underestimated if the true sister group of bats (whatever taxon that may be) is absent from a study. These possibilities indicate that sampling methods must be considered when interpreting results of phylogenetic analyses.

Results of Biochemical and Molecular Studies

A wide variety of biochemical and molecular data have been used in attempts to resolve bat relationships (table 1). Some studies have produced inconclusive results, but the majority support monophyly of Chiroptera. In no case have molecular data provided unambiguous support for bat diphyly.

Immunological Distance Data and DNA-DNA Hybridization

The use of immunological data in studies of higher-level relationships of mammals was reviewed recently by Sarich (1993). Cronin and Sarich (1980) reported that albumin immunological distance data from bats and members of four other mammalian orders provide clear support for bat monophyly (table 1). Results of more comprehensive immunodiffusion experiments involving additional mammalian orders have never been fully reported, but Sarich (1993: 105) stated that results of such experiments "unequivocally support bat monophyly."

Kilpatrick and Nunez (1993) and Nunez and Kilpatrick (in press) have reported in abstracts the results of a DNA-DNA hybridization study that included bats and members of three other mammalian orders (table 1). Results of bootstrap analyses indicate some ambiguity in the data (Kilpatrick and Nunez, 1993), but phylogenetic trees generated from analysis of mean estimates of genetic divergence and normalized percent of hybridization were interpreted as supporting monophyly of Chiroptera (Kilpatrick and Nunez, 1993; Nunez and Kilpatrick, in press).

Amino Acid Sequences

Pettigrew et al. (1989) were the first to use amino acid sequence data to address relationships of Megachiroptera and Microchiroptera. A series of "preliminary" phylogenetic trees produced from analyses of β-globin amino acid sequences in bats and members of seven other mammalian orders were interpreted by Pettigrew et al. (1989) as supporting bat diphyly. However, Baker et al. (1991b) disagreed with that interpretation, pointing out that diphyly of Microchiroptera and Primates—rather than Chiroptera—was indicated by topology of the β-globin trees. Pettigrew (1991a) added several taxa (and apparently some α-globin sequences) to the data set, and upon reanalysis concluded that the hemoglobin data are ambiguous concerning bat relationships.

The hemoglobin studies discussed by Pettigrew and his colleagues are difficult to interpret because the data have never been published, and it is not entirely clear which globin sequences were considered by Pettigrew (1991a). In other studies, Stanhope et al. (1993) reported that analyses including both α-globin and β-globin amino acid sequences provide support for bat monophyly. Stanhope et al. (1993) argued that Pettigrew (1991a) had used exactly the same α-globin and β-globin data employed in their studies, but that his analytical procedures had not

allowed him to identify the most parsimonious tree for the subset of taxa analyzed. Stanhope et al.'s (1993) reanalysis of this data subset (α- and β-globin from 52 mammal species) indicated monophyly of Chiroptera, although support for this grouping was weak. In trees only one step longer than the shortest tree, two clades of bats (one containing vespertilionids and another containing the remaining megachiropterans and microchiropterans) apparently occur as separate branches at an unresolved node, thus suggesting that both Chiroptera and Microchiroptera might be paraphyletic. Bat monophyly sensu Pettigrew et al. (1989) was not supported in any of the near most parsimonious trees examined by Stanhope et al. (1993).

Analyses of more comprehensive amino acid sequence data sets (including data from α- and β-globins, myoglobins, lens αA crystallins, fibrinopeptides, cytochrome c, ribonucleases, and embryonic α- and β-globins) also provide weak support for bat monophyly (Czelusniak et al., 1990; Stanhope et al., 1993). A phylogenetic tree published by Czelusniak et al. (1990: fig. 3) indicated paraphyly of Chiroptera, but in the text (p. 565) the authors noted that addition of α- and β-globin data from another microchiropteran (*Tadarida*) changes the tree topology so that Chiroptera is monophyletic. The evidence placing bats together within this tree must have come principally from α- and β-globin data, as these were the only proteins sampled in multiple bat species (Czelusniak et al., 1990).

de Jong et al. (1993) reported results of a study of αA-crystallin amino acid sequences from bats and members of 17 other mammalian orders (table 1). Among the mammals considered, sequence variation in the αA-crystallin chain occurs at 62 positions (de Jong et al., 1993: table 2.1), and substitutions at 32 of these positions may be phylogenetically informative. Parsimony analysis of this data set suggests bat diphyly, but only two additional steps are required to place bats together in a monophyletic group (de Jong et al., 1993). Because data from only three bat species (*Pteropus vampyrus, P. scapulatus,* and *Artibeus jamaicensis*) were included in the study, and only a single unambiguous sequence transformation supported bat diphyly, de Jong et al. (1993: 9) concluded that the αA-crystallin sequence data were "indecisive as to the mono- or biphyletic origin of Micro- and Megachiroptera."

rDNA Restriction Sites

Baker et al. (1991a) mapped 52 rDNA restriction sites in bats and members of four other mammalian orders (table 1). A total of 28 variable sites were identified, including 17 that were potentially phylogenetically informative (Baker et al., 1991a). Unfortunately, relationships of Megachiroptera and Microchiroptera could not be resolved using this data set. A tree consistent with bat diphyly sensu Pettigrew et al. (1989) was found to be one step shorter than the bat monophyly tree presented by Wible and Novacek (1988), but this difference was interpreted as insignificant (Baker et al., 1991a, 1991b). Parsimony analysis resulted in discovery of numerous trees two steps shorter than the "bat diphyly" tree, and a strict consensus of these produced a poorly resolved tree which indicated nonmonophyly of Primates and Microchiroptera as well as Chiroptera (Baker et al., 1991a). Pettigrew's (1991a) claims to the contrary, the rDNA restriction site data presented to date do not appear to provide a useful guide to higher-level relationships among archontan mammals.

DNA Sequences

Although most studies of DNA sequences have included comparatively small numbers of taxa (table 1), these studies have generally produced conclusive results. Strong support for bat monophyly has come from nucleotide sequence analyses of two nuclear genes, the ϵ-globin gene (Bailey et al., 1992) and the gene for interphotoreceptor retinoid binding protein (Stanhope et al., 1992, 1993). Chiropteran monophyly has also been supported by analyses of nucleotide sequence data from two mitochondrial genes, the cytochrome oxidase subunit II gene (Adkins and Honeycutt, 1991, 1993), and the 12S rDNA gene (Mindell et al., 1991; Ammerman and Hillis, 1992; Knight and Mindell, 1993; Springer and Kirsch, 1993).

Bailey et al. (1992) considered the nuclear ϵ-globin gene (the 5'-most member of the

TABLE 1

Summary of Biochemical and Molecular Studies

Study	Data	Taxa	Conclusions
Cronin and Sarich (1980)	Albumin immunological distances	3 microbats, 1 megabat, 5 primates, 1 dermopteran, 1 scandentian, 3 edentates, + other unspecified taxa	Bats monophyletic
Sarich (1993)	Albumin immunological distances	Unspecified taxa including members of all mammalian orders	Bats monophyletic
Kilpatrick and Nunez (1993); Nunez and Kilpatrick (in press)	DNA-DNA hybridization	Unspecified taxa including microbats, megabats, primates, insectivorans, and edentates	Bats monophyletic[a]
Pettigrew et al. (1989)	β-globin amino acid sequences	6 microbats, 4 megabats, 10 primates, 1 scandentian, 2 carnivores, 3 rodents, 3 perissodactyls, 2 artiodactyls, 1 edentate	Bats diphyletic/inconclusive[b]
Pettigrew (1991a)	Hemoglobin amino acid sequences[c]	11 microbats, 4 megabats, 10 primates, 1 scandentian, 3 carnivorans, 3 rodents, 3 perissodactyls, 1 hyracoid, 1 proboscidean, 4 artiodactyls, 3 cetaceans, 3 insectivorans, 1 edentate, 1 marsupial, 2 monotremes	Inconclusive/bats monophyletic[c]
Czelusniak et al. (1990); Stanhope et al. (1993)	α- and β-globin amino acid sequences + data from other proteins[d]	4 microbats, 2 megabats, 21 primates, 1 scandentian, 13 carnivorans, 7 rodents, 1 lagomorph, 4 perissodactyls, 1 hyracoid, 1 sirenian, 2 proboscideans, 3 cetaceans, 10 artiodactyls, 3 insectivorans, 1 edentate, 2 marsupials, 2 monotremes, 8 birds, 4 reptiles, 2 amphibians, 5 fishes	Bats monophyletic
Stanhope et al. (1993)	α- and β-globin amino acid sequences	11 microbats, 4 megabats, 27 primates, 1 scandentian, 22 carnivorans, 10 rodents, 1 lagomorph, 5 perissodactyls, 1 hyracoid, 1 sirenian, 2 proboscideans, 3 cetaceans, 13 artiodactyls, 1 tubulidentate, 3 insectivorans, 2 edentates, 2 marsupials, 2 monotremes, 23 birds, 6 reptiles, 1 amphibian, 4 fishes	Bats monophyletic[e]

TABLE 1—(*Continued*)

Study	Data	Taxa	Conclusions
de Jong et al. (1993)	αA-crystallin amino acid sequences	1 microbat, 2 megabats, 7 primates, 1 scandentian, 9 carnivorans, 10 rodents, 2 lagomorphs, 1 macroscelidean, 3 perissodactyls, 1 hyracoid, 1 sirenian, 1 proboscidean, 3 cetaceans, 5 artiodactyls, 1 tubulidenate, 1 pholidotan, 1 insectivoran, 3 edentates, 2 marsupials, 1 bird, 2 reptiles, 1 amphibian, 1 fish	Bats diphyletic/inconclusive[f]
Baker et al. (1991a)	rDNA restriction sites	14 microbats, 5 megabats, 2 primates, 1 dermopteran, 1 rodent, 2 insectivores	Inconclusive
Bailey et al. (1992); Stanhope et al. (1993)	ε-globin gene nucleotide sequences	1 microbat, 1 megabat, 11 primates, 1 dermopteran, 1 scandentian, 1 lagomorph, 1 artiodactyl	Bats monophyletic[g]
Stanhope et al. (1992, 1993)	Interphotoreceptor retinoid binding protein (IRBP) gene nucleotide sequences	2 microbats, 1 megabat, 3 primates, 1 dermopteran, 1 scandentian, 1 carnivoran, 1 rodent, 1 lagomorph, 1 artiodactyl, 1 marsupial	Bats monophyletic[g]
Adkins and Honeycutt (1991, 1993)	Cytochrome oxidase subunit II gene (COII) nucleotide sequences	1 microbat, 1 megabat, 2 primates, 1 dermopteran, 1 scandentian, 1 rodent, 1 artiodactyl, 1 edentate (an additional 2 microbats, 1 rodent, 1 artiodactyl, and 1 macroscelidean were added in the 1993 analysis)	Bats monophyletic[h]
Mindell et al. (1991); Knight and Mindell (1993)	12S rDNA and cytochrome oxidase subunit I (COI) gene nucleotide sequences	1 microbat, 1 megabat, 1 primate, 1 rodent, 1 bird	Bats monophyletic[i]
Ammerman and Hillis (1992)	12S rDNA gene nucleotide sequences	2 microbats, 2 megabats, 1 primate, 1 dermopteran, 1 scandentian, 1 rodent, 1 artiodactyl, 1 edentate, 1 marsupial	Bats monophyletic[j]
Springer and Kirsch (1993)	12S rDNA gene nucleotide sequences	1 microbat, 1 megabat, 1 primate, 1 carnivoran, 1 lagomorph, 4 rodents, 1 cetacean, 5 artiodactyls, 1 perissodactyl,	Bats monophyletic/inconclusive[k]

TABLE 1—(*Continued*)

Study	Data	Taxa	Conclusions
		1 hyracoid, 1 sirenian, 1 proboscidean, 1 edentate, 3 marsupials, 2 monotremes	
Honeycutt and Adkins (1993)	COII, IRBP, and ϵ-globin gene nucleotide sequences	1 composite microbat, 1 composite megabat, 3 primates, 1 dermopteran, 1 scandentian, 1 lagomorph, 1 composite artiodactyl	Bats monophyletic

[a] This study has been reported only in abstracts, so the conclusions should be considered preliminary.

[b] Pettigrew et al. (1989) claimed that these data supported bat diphyly, but Baker et al. (1991b) pointed out that diphyly of Microchiroptera and Primates (rather than Chiroptera) was indicated by the trees presented by Pettigrew and his colleagues. Baker et al. (1991b) concluded that the data employed were inconclusive regarding bat monophyly.

[c] Pettigrew (1991a) referred to this data set as containing "hemoglobin" data but did not specify the type or source of these data. Stanhope et al. (1993) argued that this data set contained a combination of α-globin and β-globin data, exactly the same data employed in their study. When Stanhope et al. (1993) analyzed the same set of 52 species, they found that the data support monophyly of bats contra Pettigrew (1991a).

[d] The complete data set used in these studies includes data from several proteins (α- and β-globins, myoglobins, lens αA crystallins, fibrinopeptides, cytochrome c, ribonucleases, and embryonic α- and β-globins), but only α-globin and β-globin data were sampled in both megachiropteran and microchiropteran bats. Some of the taxa listed are known from either α-globin or β-globin but not both. Taxa known only from other proteins have been omitted from the list of taxa given here.

[e] The most parsimonious tree identified in this analysis supported bat monophyly, but possible paraphyly of both Chiroptera and Microchiroptera was indicated by trees only one step longer (Stanhope et al., 1993).

[f] Parsimony analysis of this data set suggested bat diphyly, but only two additional steps were required to place bats together in a monophyletic group. Because so few bats were included in the study, and only a single unambiguous sequence transformation supported bat diphyly, de Jong et al. (1993: 9) concluded that the αA-crystallin sequence data were "indecisive as to the mono- or biphyletic origin of Micro- and Megachiroptera."

[g] Stanhope et al. (1993) used a one-tailed binomial test to demonstrate that these phylogenetic results were statistically significant.

[h] Bats appeared monophyletic in analyses based on transversions only; analyses including both transitions and transversions resulted in a nonmonophyletic Chiroptera. Bat diphyly sensu Pettigrew et al. (1989) was not supported in any tree, however.

[i] Analyses of combined data from 12S rDNA and cytochrome oxidase subunit I (COI) gene sequences supported bat monophyly when only transversions were considered; Chiroptera did not appear monophyletic when both transitions and transversions were included in the analysis. When the two genes were analyzed separately, the 12S data strongly supported bat monophyly, but the COI data were inconclusive. Bat diphyly sensu Pettigrew et al. (1989) was not supported in any of the analyses.

[j] Chiroptera appeared as a monophyletic group in all analyses (transversions only, transitions + transversions). A variety of statistical methods (i.e., g_1 statistic, bootstrapping, Templeton's test, T-PTP) were employed to demonstrate that these phylogenetic results were statistically significant.

[k] Support for bat monophyly was found when both transitions and transversions were considered, but diphyly was indicated in a transversion-only analysis. Bat diphyly sensu Pettigrew et al. (1989) was not supported in any of the analyses. The authors concluded that bat monophyly received "mixed support" in this study (Springer and Kirsch, 1993: 149), but a more equitable conclusion is that these data were inconclusive with respect to bat monophyly (see text).

β-globin gene cluster) to be appropriate for investigating bat relationships because this gene appears to have been less prone to tandem duplications than other β-type globin genes, and because most of the ϵ-globin sequence is noncoding and thus presumably not subject to functional constraints. Over 1200 nucleotide positions of the ϵ-globin sequence were sampled in bats and members of five other mammalian orders (table 1; Bailey et al., 1992). Analysis of this data set resulted in identification of a single most parsimonious tree which supported monophyly of Chiroptera (Bailey et al., 1992; Stanhope et al., 1993). Trees indicating bat diphyly sensu Pettigrew et al. (1989) were found to require over 100 additional evolutionary steps (nucleotide substitutions) than the shortest tree (Bailey et al., 1992). Megachiroptera and Microchiroptera uniquely share 39 derived substitutions in the ϵ-globin sequence, including 26 substitutions that exhibit no homoplasy in the context of the data set (Bailey et al., 1992; Stanhope et al., 1993). In contrast, only two substitutions potentially support a megachiropteran-primate clade or a megachiropteran-dermopteran clade.

The gene for interphotoreceptor retinoid binding protein (IRBP) is a single-copy nuclear gene (Stanhope et al., 1992, 1993). Stanhope et al. (1992) argued that functionally constrained coding DNA sequences such as IRBP may be particularly useful for resolving ancient phylogenetic branching patterns because the relatively low sequence divergence seen in such genes facilitates alignment of sequences from divergent mammalian orders. IRBP sequences of approximately 1200 base pairs were collected from bats and members of eight other mammalian orders (table 1; Stanhope et al., 1992). Analyses of these data were conducted under a series of different assumptions (neighbor-joining and parsimony, rooted and unrooted trees, marsupials present or absent in data set), and all results strongly supported bat monophyly (Stanhope et al., 1992). In an unrooted parsimony analysis of the eutherian taxa, the shortest tree indicating bat diphyly sensu Pettigrew et al. (1989) required 46 more nucleotide substitutions than the most parsimonious trees (Stanhope et al., 1992). A total of 22 nucleotide substitutions (7 of which were unique in the data set) were identified as synapomorphies of Chiroptera (Stanhope et al., 1992, 1993).

Adkins and Honeycutt (1991, 1993) compared nucleotide sequences of 684 base pairs of the mitochondrial cytochrome oxidase subunit II gene (COII). The 1991 study included two bat species and members of six other mammalian orders; the 1993 version included four bats and members of seven other orders (table 1). Analyses of the COII data with transversions and transitions weighted equally suggested chiropteran paraphyly in both iterations of the study. In the 1991 analysis, a rodent nested within the smallest clade containing both bats in the most parsimonious trees (Adkins and Honeycutt, 1991: fig. 1A). In contrast, bats, primates, and artiodactyls formed a clade in four equally parsimonious trees discovered in the 1993 study; monophyly of Artiodactyla and Primates was supported in all four of these trees, but Primates nested within the smallest clade containing all four bats (Adkins and Honeycutt, 1993: fig. 3). Microchiroptera appeared as a paraphyletic group in all equally parsimonious trees, with *Rhinolophus* appearing as the sister taxon of Primates rather than grouping with the other microchiropterans (Adkins and Honeycutt, 1993). However, different results were obtained when an alternative weighting system was employed.

In both interations of Adkins and Honeycutt's study, the most parsimonious trees based on transversions-only data contained a monophyletic Chiroptera. Ten nucleotide substitutions supported Chiroptera in the 1991 study, while seven substitutions supported this group in the 1993 version (Adkins and Honeycutt, 1991, 1993). In the 1993 study, which included three microchiropterans, the topology reconstructed using the transversions-only data is consistent with current hypotheses of microchiropteran phylogeny (e.g., Van Valen, 1979; Luckett, 1980b; Smith, 1980; Pierson, 1986). Microchiroptera forms a monophyletic group, and *Macrotus* and *Phyllostomus* (members of the monophyletic family Phyllostomidae) together form a well-supported clade within Microchiroptera (Adkins and Honeycutt, 1993: fig. 3).

Studies of mitochondrial genes frequently

employ transversion weighting, which is generally justified based on the expectation that mitochondrial DNA transition/transversion ratios decrease and transition substitutions approach saturation as evolutionary divergence increases (Adkins and Honeycutt, 1991; Mindell et al., 1991). Because the divergence times for bats and their possible relatives are quite long (55–70 million years; Benton, 1990), transversion weighting has been judged to be appropriate by most molecular systematists testing bat monophyly with mitochondrial DNA data (e.g., Adkins and Honeycutt, 1991, 1993; Mindell et al., 1991; Ammerman and Hillis, 1992; Knight and Mindell, 1993; Springer and Kirsch, 1993).

The technique most commonly used to effect transversion weighting is simple omission of transitions from the analysis (e.g., Adkins and Honeycutt, 1991, 1993; Mindell et al., 1991; Ammerman and Hillis, 1992). However, questions have been raised recently concerning this method (Springer and Kirsch, 1993; Novacek, 1994; Wheeler, in press). Sample size is one area of potential weakness. Springer and Kirsch (1993) pointed out that transversion weighting may be problematic when applied to short sequences (e.g., $\leq$400 base pairs) because of the relatively small number of transversions preserved in such sequences. Effectively discarding potentially informative data (i.e., transitions) may be hard to justify in many cases.

Wheeler (in press) and Novacek (1994) advocate application of a spectrum of weights to transversions in order to discover the threshold values that affect tree topologies. Novacek (1994) reanalyzed the COII data from Adkins and Honeycutt's (1991) study and found that bat monophyly was maintained when transversions were given weights either 10× or 5× that of transitions, but the bat clade collapsed when transversions were weighted 2× transitions. The fact that relatively low transversion/transition weighting ratios (e.g., 5:1) produce trees in which Chiroptera is monophyletic may be interpreted as providing strong support for bat monophyly.

Mindell et al. (1991) analyzed sequence data from mitochondrial 12S rDNA (744 base pairs) and cytochrome oxidase subunit I genes (COI; 236 base pairs) in two bats and members of two other mammalian orders. Preliminary analyses in which transitions and transversions were weighted equally indicated that bats were not monophyletic. However, when only transversions were considered, Mindell et al. (1991) found clear support for bat monophyly even when the outgroup was varied, alternative alignment strategies were employed, and a gap-coding scheme was used. When the two data subsets were considered separately, the 12S data strongly supported bat monophyly, but the COI data were ambiguous. Knight and Mindell (1993) examined the 12S data for substitution biases, and found that transversions involving G (guanine) were relatively rare and occurred far below expected levels. Suggesting that these rare substitutions may be particularly useful for resolving branching patterns of ancient divergences, Knight and Mindell (1993) noted that two such transversions support bat monophyly, while no substitutions of this type support a megachiropteran + primate clade.

Ammerman and Hillis (1992) also analyzed mitochondrial 12S rDNA nucleotide sequences. While Mindell et al. (1991) considered a relatively large number of base pairs, the taxonomic sampling in that study was very poor (table 1). In contrast, Ammerman and Hillis (1992) considered a larger sample of taxa (four bats and members of seven other mammalian orders), but analyzed a shorter sequence of only 257 base pairs (table 1). An unrooted analysis of these data with transitions and transversions weighted equally resulted in two equally parsimonious trees, each of which supported bat monophyly (Ammerman and Hillis, 1992). Employing several quantitative measures of confidence that can be placed on a hypothesis in the context of a particular data set (e.g., g_1 statistic, bootstrapping, Templeton's test, T-PTP), Ammerman and Hillis (1992) demonstrated that their phylogenetic results were statistically significant. Additional rooted and unrooted analyses including only transversion data also supported bat monophyly (Ammerman and Hillis, 1992). In the unrooted analyses, eight or nine substitutions (six of which were unique in the data set) separated bats from the other mammals in the tree (Ammerman and Hillis, 1992).

A third analysis of 12S rDNA data was conducted by Springer and Kirsch (1993). These authors analyzed a data set of 412 base pairs in two bats and members of 13 other mammalian orders (table 1). While this study included more taxa and longer nucleotide sequences than that of Ammerman and Hillis (1992), the goal of Springer and Kirsch's study was evaluation of paenungulate relationships, not bat monophyly, and their taxonomic sampling was limited with respect to archontan mammals. Members of Dermoptera and Scandentia were not included in the study, and the bat suborders were each represented by only a single species (Springer and Kirsch, 1993). An analysis of the 12S data including all substitutions (transversions and transitions) resulted in a monophyletic Chiroptera in each of four equally parsimonious shortest trees (Springer and Kirsch, 1993: fig. 2). However, some trees only one step longer did not support bat monophyly, and a bootstrap analysis could not resolve the relationships of bats at a 50 percent level (Springer and Kirsch, 1993). Another analysis based exclusively on transversion data failed to support bat monophyly. *Eptesicus* (a microchiropteran) grouped with a cetacean in all ten of the shortest trees, and *Macroglossus* (a megachiropteran) grouped with an edentate in nine of the ten trees (Springer and Kirsch, 1993: fig. 4). Weak support for bat monophyly was found in a third analysis using Lake's method of invariants applied to a data set that included the bats, a primate, and a marsupial + monotreme group (Springer and Kirsch, 1993). Based on all of their analyses, Springer and Kirsch (1993: 149) concluded that bat monophyly received "mixed support" in their study. While it is clear that bat diphyly sensu Pettigrew et al. (1989) was not supported in any of Springer and Kirsch's (1993) analyses, there also seems to be little clear support for bat monophyly. Especially given the small number of bat species included in this study, a more appropriate interpretation of the data and results may be that they are inconclusive with respct to the issue of bat monophyly.

Honeycutt and Adkins (1993) combined sequences from three genes (COII, IRBP, and ϵ-globin) in a single, large data set. Bats and members of five other mammalian orders were included in the study (table 1). Chiropteran monophyly was supported in an unrooted parsimony analysis based on all substitutions, and also in an alternative analysis including only transversions (Honeycutt and Adkins, 1993).

Results of Morphological Studies

Numerous morphological studies have been conducted in recent years, and the majority of these support bat monophyly (table 2). The data employed include features of fetal membranes, wing musculature, postcranial and cranial osteology, vascular system, volume of brain components, and combinations of these and other data. Only two data subsets apparently support bat diphyly: features of the nervous system (Pettigrew, 1986, 1991a, 1991b; Pettigrew et al., 1989; Johnson and Kirsch, 1993) and of the penis (Smith and Madkour, 1980). The results of relevant morphological studies of bat relationships are summarized below; putative morphological synapomorphies of Chiroptera are discussed in a subsequent section.

Smith and Madkour (1980) investigated structure of the penis in bats and members of five other mammalian orders, and combined the penis data with characters from other anatomical systems in a phylogenetic analysis. Smith and Madkour (1980) identified two derived features of the penis, two brain characters, one dental character, and one feature of the wrist that Megachiroptera apparently shares with taxa other than Microchiroptera (i.e., Dermoptera, Primates, and Scandentia). Lack of similarity of conditions lumped together by Smith and Madkour (1980: 360–361) has resulted in rejection of two of these putative synapomorphies, "enlarged neocortex" and "derived, non-insectivorous dentition" (Wible and Novacek, 1988; see also Henson, 1970; Campbell, 1980; Koopman and MacIntyre, 1980). A third character ("distal radius and lunar carpal broadened") was discussed and rejected by Wible and Novacek (1988) because the distribution and potential homologies of these modifications were not as indicated by Smith and Madkour (1980). The remaining characters—two features of the penis and one brain

TABLE 2
Summary of Morphological Studies

Study	Data	Taxa	Conclusions
Smith and Madkour (1980)	Penis + other characters[a]	150 species of bats including both megabats and microbats, 7 primates, 1 dermopteran, 1 scandentian, 4 insectivorans, 1 edentate	Bats diphyletic
Pettigrew et al. (1989); Pettigrew (1991a)	Nervous system[b]	11 microbats, 9 megabats, 4 primates, 1 dermopteran, 1 scandentian, 1 rodent, 4 macroscelideans, 1 hyracoid, 1 edentate	Bats diphyletic
Johnson and Kirsch (1993)	Nervous system[c]	2 microbats, 2 megabats, 7 primates, 2 dermopterans, 1 scandentian, 5 carnivorans, 6 rodents, 1 macroscelidean, 1 lagomorph, 2 perissodactyls, 1 hyracoid, 1 sirenian, 1 cetacean, 4 artiodactyls, 4 insectivorans, 4 edentates, 11 marsupials, 2 monotremes	Bats diphyletic
	Nervous system + diverse morphological characters from Novacek et al. (1988)[d]	Same as above; data from Novacek et al. (1988) reported for each order (species examined not specified)	Bats monophyletic
Lapoint and Baron (1993)	Volume of brain components[e]	60 microbats, 20 megabats, 120 primates	Bats monophyletic[e]
Luckett (1980b)	Fetal membranes + other characters[f]	Unspecified microbats (including members of at least 10 families), megabats, dermopterans, primates, and scandentians[g]	Bats monophyletic
Luckett (1993)	Fetal membranes + basicranium[h]	Unspecified microbats (including members of at least 10 families), megabats, dermopterans, primates, scandentians, rodents, and lagomorphs[g]	Bats monophyletic
Thewissen and Babcock (1991)	Propatagial muscles	2 microbats, 1 megabat, 1 dermopteran	Bats monophyletic[i]
Thewissen and Babcock (1993)	Propatagial muscles + cephalic vein	4 microbats, 3 megabats, 1 dermopteran, 1 rodent, 1 marsupial, 1 bird	Bats monophyletic[i]
Beard (1993a)	Postcranial, cranial and dental morphology[j]	Unspecified microbats, megabats, fossil and extant primates, dermopterans, paromomyids, micromomyids, plesiadapids, and scandentians[g]	Bats monophyletic
Szalay and Lucas (1993)	Postcranial and cranial morphology	Unspecified microbats, megabats, fossil and extant primates, dermopterans, paromomyids, mixodectids, microsyopids, plesiadapids, and scandentians	Bats monophyletic[i]

TABLE 2—(*Continued*)

Study	Data	Taxa	Conclusions
Kay et al. (1992)	Cranial morphology[k]	7 microbats, 3 megabats, 5 primates, 1 plesiadapid, 1 paromomyid, 1 dermopteran, 2 scandentians, 3 insectivorans, and *Asioryctes*	Bats monophyletic
Wible and Novacek (1988)	Cranial morphology + diverse morphological characters from other systems[l]	Unspecified microbats, megabats, primates, dermopterans, scandentians, + members of other mammalian orders	Bats monophyletic
Wible and Martin (1993)	Basicranial morphology[m]	Unspecified microbats, megabats, fossil and extant primates, plesiadapids, paromomyids, dermopterans, and scandentians	Bats monophyletic
Simmons (1993)	Diverse morphological characters[n]	Unspecified microbats, megabats, primates, plesiadapids, paromomyids, micromomyids, dermopterans, and scandentians	Bats monophyletic

[a] Although this study focused on morphology of the penis, two characters of the nervous system, one dental character, and two characters of the forelimb were included in the phylogenetic analysis.

[b] 24 characters of the nervous system were analyzed in the explicit cladistic analysis. One postcranial character was discussed extensively by Pettigrew et al. (1989), and several undescribed neural features were mentioned by Pettigrew (1991a).

[c] A total of 29 characters of the nervous system were considered in this analysis. These data include 24 characters previously described by Johnson et al. (1982a, 1982b, in press), and 5 characters taken from Pettigrew et al. (1989).

[d] A total of 94 characters were considered in this study, including the 29 neural characters mentioned in footnote *c* plus 65 morphological characters from diverse morphological systems. The latter data were taken from Novacek et al. (1988).

[e] This study apparently comprised a statistical comparison of volumes of 12 brain components in different taxa. The study has been reported only in an abstract, so the data have not been published and the results must be considered preliminary.

[f] The phylogenetic analysis included 7 fetal membrane characters, 1 character of the female urogenital tract, and 5 characters of the forelimb.

[g] These taxa were included in the cladistic analysis; unspecified members of other mammalian orders were considered when polarizing characters.

[h] 16 characters of the fetal membranes and 1 basicranial character were included in the phylogenetic analysis.

[i] No explicit parsimony analysis was conducted in this study.

[j] A total of 29 characters were considered in this study, including 21 postcranial characters, 6 cranial characters, and 1 dental feature.

[k] 33 cranial characters were included in this study.

[l] A total of 36 characters were listed as supporting the relationships hypothesized in this study, including 16 postcranial characters, 15 cranial characters, 3 features of the fetal membranes, 1 character of the penis, and 1 brain character.

[m] A total of 15 basicranial characters were discussed in this study. No formal parsimony analyses of these data were conducted.

[n] Data were drawn directly from previous studies; redundant characters were removed, but no attempt was made to modify character descriptions or coding. The data included 6 categories of characters: cranial features excluding auditory region (33 characters), auditory region (20 characters), anterior axial skeleton and forelimb (31 characters), hindlimb (35 characters), reproductive tract and fetal membranes (12 characters), and nervous system (23 characters). Sources of data were: Johnson et al. (1982a, 1982b); Luckett (1977, 1980a, 1980b, 1985); MacPhee et al. (1988); Novacek (1980a, 1985b, 1986); Smith and Madkour (1980); Wible and Novacek (1988); and Pettigrew et al. (1989).

character—provide potential support for the bat diphyly hypothesis.

In the late 1980s Pettigrew and his colleagues reported a series of derived features of the nervous system that suggest that bats are diphyletic (Pettigrew, 1986, 1991a, 1991b; Pettigrew and Cooper, 1986; Pettigrew and Jamieson, 1987; Pettigrew et al., 1989). Over 20 derived neural traits and one postcranial character have thus far been cited by this group in support of bat diphyly (see summary in Pettigrew, 1991a). Details of several of the characters employed in this study have been questioned by various authors (e.g., Wible and Novacek, 1988; Baker et al., 1991b; Simmons et al., 1991; Thiele et al., 1991; Johnson and Kirsch, 1993; Kaas and Preuss, 1993; Simmons, 1993), but it seems clear that neural characters as a group strongly support bat diphyly. This conclusion is also supported by alternative analyses recently conducted by Johnson and Kirsch (1993).

Johnson, Kirsch, and their colleagues are responsible for a series of influential papers entitled "Phylogeny Through Brain Traits" (Switzer et al., 1980; Johnson et al., 1982a, 1982b, 1984, in press; Kirsch, 1983; Kirsch and Johnson, 1983; Kirsch et al., 1983). In a reanalysis of data described in these publications, Johnson and Kirsch (1993) found that their neural characters (many of which differ from those employed by Pettigrew and his colleagues) support bat diphyly. Addition of five characters from Pettigrew's data set changed topology of the most parsimonious tree somewhat, but diphyly of bats was still supported when only neural characters where considered in the analysis (Johnson and Kirsch, 1993). However, when neural data (29 characters) were combined with data from other anatomical systems (65 characters from Novacek et al., 1988), the results were strikingly different—bats formed a monophyletic group in the most parsimonious tree (Johnson and Kirsch, 1993). Specifics of the synapomorphies supporting Chiroptera were not discussed by these authors.

One additional study focusing on brain morphology and bat phylogeny has been reported but details of this work have not yet been published. Lapoint and Baron (1993) described in an abstract the results of morphometric comparisons of volumes of 12 brain components in bats and primates. Unspecified methods were used to derive phylogenetic trees from these data, and statistical methods were employed to compare these trees with the monophyletic and diphyletic models. According to Lapoint and Baron (1993: 64), their ". . . results corroborate the monophyletic scenario in every situation . . . The diphyletic model, on the other hand, was found to be as likely as a random phylogeny would be." However, these results must be considered preliminary until a detailed account of this study has been published.

Luckett (1977, 1980a, 1980b, 1985, 1993) extensively studied patterns of fetal membrane formation in mammals and interpreted these ontogenetic and morphological data in a phylogenetic context. To evaluate bat relationships, Luckett (1980b) developed a character set of features of fetal membranes and the forelimb, surveyed these characters in extant archontan mammals (table 2), assessed polarity by reference to numerous other mammalian orders, and conducted a manual cladistic analysis of these data. Results of this study indicate that bats are monophyletic; putative synapomorphies of Chiroptera include four derived features of the forelimb and two features of the fetal membranes (Luckett, 1980b). Luckett (1993) subsequently conducted a revised analysis which included data from fetal membranes and the basicranium in archontans, rodents, and lagomorphs. Results of this new analysis similarly supported chiropteran monophyly, and three uniquely derived features of fetal membranes were interpreted as synapomorphies of bats (Luckett, 1993).

Wible and Novacek (1988) described several new features of the skull and vascular system of bats, reviewed the literature on bat morphology and phylogeny, and summarized data supporting bat monophyly. Their review effectively considered all data relevant to the bat monophyly controversy that had been published as of 1987 (e.g., Luckett, 1980b; Smith and Madkour, 1980; Calford et al., 1985; Pettigrew, 1986; Pettigrew and Cooper, 1986). A total of 22 derived features supporting bat monophyly were identified by Wible and Novacek (1988: table 3), including six cranial characters, nine osteological features of the postcranium, three muscular

characters, three features of the fetal membranes, and one neural character. Although the cranial characters were rejected by Pettigrew et al. (1989: table 8), criticisms leveled at these characters did not adequately address issues of homology and the possibility of reversals within higher taxa (Baker et al., 1991b; Wible and Martin, 1993). Baker et al. (1991b) published a tabular summary of the putative bat synapomorphies reviewed by Wible and Novacek (1988) and added five postcranial features to the list. However, these additional characters were not discussed further by Baker et al. (1991b) and they have never been properly described or evaluated.

Thewissen and Babcock (1991, 1993) investigated morphology and innervation of the propatagial muscle complex of bats and other volant mammals (table 2). Wible and Novacek (1988) had listed "occipitopollicalis muscle present on leading edge of propatagium" as a synapomorphy of bats, but Pettigrew et al. (1989) rejected this character on the grounds that other volant mammals have propatagial muscles as well. In 1991 Thewissen and Babcock identified a uniquely derived pattern of innervation in the propatagial muscle of bats (m. occipitopollicalis) that suggests that presence of this muscle is indeed a synapomorphy of Chiroptera. Expanding their study to include additional taxa and other features of the propatagium (table 2), Thewissen and Babcock (1993) confirmed the uniquely shared pattern of muscle innervation, and went on to identify two additional features that indicate a single evolutionary origin for the propatagial muscle in bats. These data were interpreted as supporting monophyly of Chiroptera (Thewissen and Babcock, 1991, 1993).

In order to evaluate the phylogenetic relationships of a variety of extinct archontans, Beard (1993a) developed a data set of postcranial, cranial, and dental characters which he surveyed in both extant and extinct forms (table 2). An exhaustive parsimony analysis of these data resulted in discovery of a single most parsimonious tree in which Chiroptera is monophyletic (Beard, 1993a). One unique cranial and six postcranial characters were identified as synapomorphies of bats (Beard, 1993a).

Szalay and Lucas (1993) also examined cranioskeletal features of fossil and living archontans, although they did not conduct an explicit parsimony analysis of their data. Based on various morphological comparisons, Szalay and Lucas (1993) concluded that Chiroptera is monophyletic, and noted several cranial and postcranial synapomorphies of bats.

Wible and Martin (1993) examined the development of the tympanic roof and floor in a variety of archontan mammals, and developed a character set based on results of their study (table 2). Although no explicit parsimony analysis was conducted, they identified two derived basicranial features that are unique to bats, confirming some of the results published earlier by Wible and Novacek (1988).

Kay et al. (1992) conducted a cladistic analysis of archontan mammals in order to assess the affinities of the extinct paromomyid *Ignacius* (table 2). For this purpose they developed a set of 33 cranial characters which could be scored in both extant and extinct groups. The fossil form *Asioryctes,* a putative primitive eutherian, was included as an outgroup to polarize characters (Kay et al., 1992). A heuristic parsimony analysis of the complete data set resulted in discovery of a monophyletic Chiroptera (Kay et al., 1992). A second abbreviated data set was compiled by assuming monophyly of Megachiroptera, Microchiroptera, Primates, and Erinaceomorpha, and scoring each with the hypothetical ancestral character states implied by the initial heuristic analysis. Not surprisingly, monophyly of bats was supported by exhaustive search analyses of this second data set, and two unique cranial synapomorphies of Chiroptera were identified. The shortest "bat diphyly" tree sensu Pettigrew et al. (1989) was found to be seven steps (17%) longer than the most parsimonious tree (Kay et al., 1992).

Simmons (1993) summarized previously published morphological character data from most of the studies described above,[2] and conducted a cladistic analysis of this integrated data set (table 2). A total of 154 characters in 6 subsets were included in Simmons'

[2] Exceptions are a number of characters described for the first time in Baker et al. (1991b), Kay et al. (1992), and Wible and Martin (1993).

(1993) study: cranial features excluding auditory region (33 characters), auditory region (20 characters), anterior axial skeleton and forelimb (31 characters), hindlimb (35 characters), reproductive tract and fetal membranes (12 characters), and nervous system (23 characters). These characters were scored in seven extant taxa (Megachiroptera, Microchiroptera, Galeopithecidae, Strepsirhini, Tarsiiformes, Anthropoidea, Scandentia) and three extinct taxa (Plesiadapidae, Paromomyidae, Micromomyidae); polarities suggested by the original author(s) of the characters were accepted for the purposes of the study. The data thus collected were analyzed under a variety of different assumptions, including different weighting systems, different approaches to taxonomic polymorphism, inclusion and exclusion of fossils, etc. Support for bat monophyly was found in every analysis (Simmons, 1993). Although some data subsets apparently support bat diphyly (neural data), paraphyly (reproductive tract + fetal membranes), or are ambiguous (auditory characters), the combined data set clearly supports bat monophyly (Simmons, 1993). Simmons warned that the results of this analysis should be considered preliminary because problems were detected with the coding schemes and polarization criteria applied to certain characters. However, subsequent analyses of a corrected data set including representatives of all of the mammalian orders have yielded the same phylogenetic results (Simmons, in prep.). The shortest "bat diphyly" trees are more than 20 steps longer than the most parsimonious trees, all of which indicate monophyly of Chiroptera (Simmons, in prep.).

Results of Studies Combining Morphological and Molecular Data

Only one study completed thus far has included both morphological and molecular data in single parsimony analysis (table 3). Novacek (1994) combined morphological data from previous studies (e.g., Luckett, 1980b; Novacek and Wyss, 1986; Novacek, 1986, 1990, 1992a; Wible and Novacek, 1988; Pettigrew et al., 1989; Thewissen and Babcock, 1991) with nucleotide sequence data from the COII gene (from Adkins and Honeycutt, 1991). A total of 49 morphological characters plus variable sites from 684 base pairs of nucleotide sequence were included in the data set (Novacek, 1994). Unweighted parsimony analysis of the entire data set (including both transitions and transversions) resulted in two equally parsimonious trees, each of which supports monophyly of Chiroptera. A second analysis involving transversions plus morphological characters (transitions omitted) produced a single most parsimonious tree that similarly supports bat monophyly (Novacek, 1994).

Summary

The molecular and morphological studies summarized above provide strong support for chiropteran monophyly (tables 1, 2, 3). Analyses of some molecular data sets have yielded ambiguous results concerning bat relationships (e.g., rDNA restriction sites, αA-crystallin amino acid sequences, COI gene sequences). However, analyses of most biochemical and molecular data support monophyly of Chiroptera (e.g., albumin immunological distances, α-globin + β-globin amino acid sequences, nuclear ϵ-globin and IRBP gene sequences, mitochondrial 12S rRNA and COII gene sequences). In no instance have molecular data provided unambiguous support for bat diphyly.

Morphological data show a slightly different pattern (table 2). Neural and penial characters generally support diphyly of bats, but other data subsets clearly support bat monophyly (e.g., characters of the cranium and postcranial skeleton, vascular system, muscles, and fetal membranes). Studies combining morphological data from many anatomical systems strongly support bat monophyly even when characters of the penis and nervous system are included in the analysis (Johnson and Kirsch, 1993; Simmons, 1993, in prep.; Novacek, 1994). Chiropteran monophyly is also supported when COII sequence data and morphological characters are combined in a single analysis (Novacek, 1994).

The most parsimonious interpretation of the diverse morphological and molecular data now available is that bats are monophyletic. In this context, characters supporting bat diphyly should be interpreted as homoplastic.

TABLE 3
Analyses Combining Morphological and Molecular Data

Study	Data	Taxa	Conclusions
Novacek (1994)	Diverse morphological data + all substitutions in COII gene nucleotide sequences[a]	Microchiroptera, Megachiroptera, Dermoptera, Strepsirhini, Anthropoidea, Artiodactyla, Rodentia, and Edentata	Bats monophyletic
	Diverse morphological data + transversions in COII sequences	Same as above	Bats monophyletic

[a] Data set included 49 morphological characters and information from 684 base pairs of the COII gene (see text for data sources). The morphological data included 14 cranial characters, 22 postcranial characters, 3 characters of the penis, 3 characters of the fetal membranes, and 7 neural characters.

Derived characters shared by megachiropterans and microchipterans represent potential synapomorphies of Chiroptera.

MORPHOLOGICAL CHARACTERS SUPPORTING BAT MONOPHYLY

As discussed above, a large number of derived morphological characters indicate that Chiroptera is a monophyletic taxon. Unfortunately, however, no adequate summary of these features is available. Some putative synapomorphies have been widely discussed in the literature, but others have been cited only in tabular summaries or have never been noted in published discussions of bat monophyly. In this section I describe those morphological features that appear to be synapomorphies of bats, review the taxonomic distribution of each feature, and discuss evidence for character polarity. Unreferenced statements concerning osteological characters are based on my examination of specimens in the collections of the AMNH (American Museum of Natural History, New York) and the USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.). Following Simmons (1993), character dependence has been hypothesized a priori only when two or more features of possible ontogenetic and/or functional dependence appear to have identical patterns of taxonomic distribution. In cases where such features do not have identical distributions, they may represent independently evolving structures and thus are described separately below.

Interpretation of some characters may vary depending on the phylogenetic placement of Chiroptera within Eutheria. All of the features listed below would be considered chiropteran synapomorphies if bats nest within Archonta with Dermoptera as their sister group (sensu Novacek and Wyss, 1986; Wible and Novacek, 1988; Novacek, 1986, 1990, 1992a, in press; Johnson and Kirsch, 1993; Szalay and Lucas, 1993; Simmons, 1993, in prep.). Some characters, however, may be considered ambiguous or plesiomorphic if Archonta is not monophyletic and bats belong elsewhere in the mammalian family tree (sensu Adkins and Honeycutt, 1991, 1993; Stanhope et al., 1992, 1993). These aspects of character interpretation are discussed separately for each character below.

DENTITION

Morphology of deciduous dentition. The deciduous dentition of eutherian mammals generally consists of incisors, canines, and premolars, all of which are replaced by second generation "adult" teeth during ontogeny. The form of the deciduous dentition is typically similar to the adult dentition. Deciduous incisors, canines, and anterior premolars resemble the teeth that will replace them, and the posterior deciduous premolars resemble adult molars in form. In all known bats, however, the anterior deciduous dentition does not resemble the permanent dentition. The deciduous incisors, canines, and first premolar are slender, projecting stylets that are markedly recurved (fig. 1; Leche, 1875; Friant, 1963; Sigé, 1991). Each tooth

has a long pedicle, and may be tipped with as many as three sharp, curved cusps. This pattern of deciduous dental morphology is unique among mammals.

Living bats also differ from other mammals in lacking molariform posterior deciduous premolars. However, some Eocene bats apparently retained molariform deciduous fourth premolars (Sigé, 1991). Because these bats show affinities with living microchiropterans (Novacek, 1987; Habersetzer and Storch, 1987, 1992; Sigé, 1991), it seems likely that primitive microchiropterans—and the most recent common ancestor of Megachiroptera and Microchiroptera—had molariform posterior deciduous premolars. Absence of these structures is derived within Chiroptera and thus is not diagnostic of bats.

Skull and Cranial Vascular System

Palatal process of premaxilla reduced; left and right incisive foramina fused in midsagittal plane. The majority of mammals have a premaxilla with a well-developed palatal process that is pierced by a pair of incisive foramina on or near the premaxillary-maxillary suture (Novacek, 1986; personal obs.). A bar of bone derived from the premaxilla extends along the midsagittal plane between the right and left incisive foramina. This presumably represents the primitive condition for mammals. In contrast, the palatal process of the premaxilla is highly modified in most bats (Dobson, 1875, 1878; Miller, 1907; Anderson, 1912; Koopman, 1984, in press; Wible and Novacek, 1988).

In megachiropteran bats the palatal process of the premaxilla is either lacking or is reduced to a small element that supports the incisor dentition but contributes little to the palate itself (Anderson, 1912; Wible and Novacek, 1988). This morphology is associated with fusion of the right and left incisive foramina to form a single opening just anterior to the palatal processes of the maxillae (Anderson, 1912; Wible and Novacek, 1988).

The palatal process of the premaxilla is also reduced in microchiropteran bats, but morphology of the anterior palate is quite variable. In most microchiropteran families the right and left incisive foramina are not separated by a median bar of bone (e.g., Rhinopomatidae, Craseonycteridae, Emballonuridae, Nycteridae, Megadermatidae, Natalidae, Thyropteridae, Vespertilionidae, and Molossidae). Exceptions include (1) Phyllostomidae, in which the incisive foramina are separated by a bar of bone connected anteriorly with the facial processes of the premaxillae; (2) some members of Mormoopidae, which have incisive foramina separated anteriorly by a very thin strut that may not be ossified; (3) Myzopodidae, which have a median bar of bone that is connected by a pair of very thin bony struts to the facial processes of the premaxillae, which do not meet at the midline; (4) Rhinolophidae, which have a median bar of bone but lack connections between this bar and the facial processes of the maxillae (facial processes of premaxilla absent); (5) some members of Mormoopidae, in which the incisive foramina are apparently reduced to tiny perforations (it is not clear if these transmit nerves or only blood vessels); and (6) Furipteridae, Mystacinidae, and Noctilionidae, which lack patent incisive foramina.

Consideration of the presumed relationships among microchiropteran families (sensu Van Valen, 1979; Pierson, 1986; Griffiths and Smith, 1991; Griffiths et al., 1992) suggests that reduction of the palatal process of the premaxilla and fusion of the incisive foramina are primitive for Microchiroptera and Chiroptera. Separation of the incisive foramina is a condition secondarily derived within bats, apparently evolving independently in phyllostomoids (1 and 2 above), myzopodids (3), and rhinolophids (4). This interpretation is supported by major differences in morphology of the anterior palate in these three groups (Dobson, 1875, 1878; Miller, 1907; Anderson, 1912; Koopman, 1984, 1994). Reduction and loss of the incisive foramina (5 and 6 above) are other derived conditions that apparently evolved well within Microchiroptera.

Among eutherian mammals, fusion of the incisive foramina is a derived condition that is limited to bats, some hominoid primates (*Homo, Pongo*), and sirenians (Kay et al., 1992; Novacek, 1986; personal obs.). In sirenians, the premaxillae are large and the palatal process is not reduced (Domning, 1978), suggesting that fusion of the incisive foram-

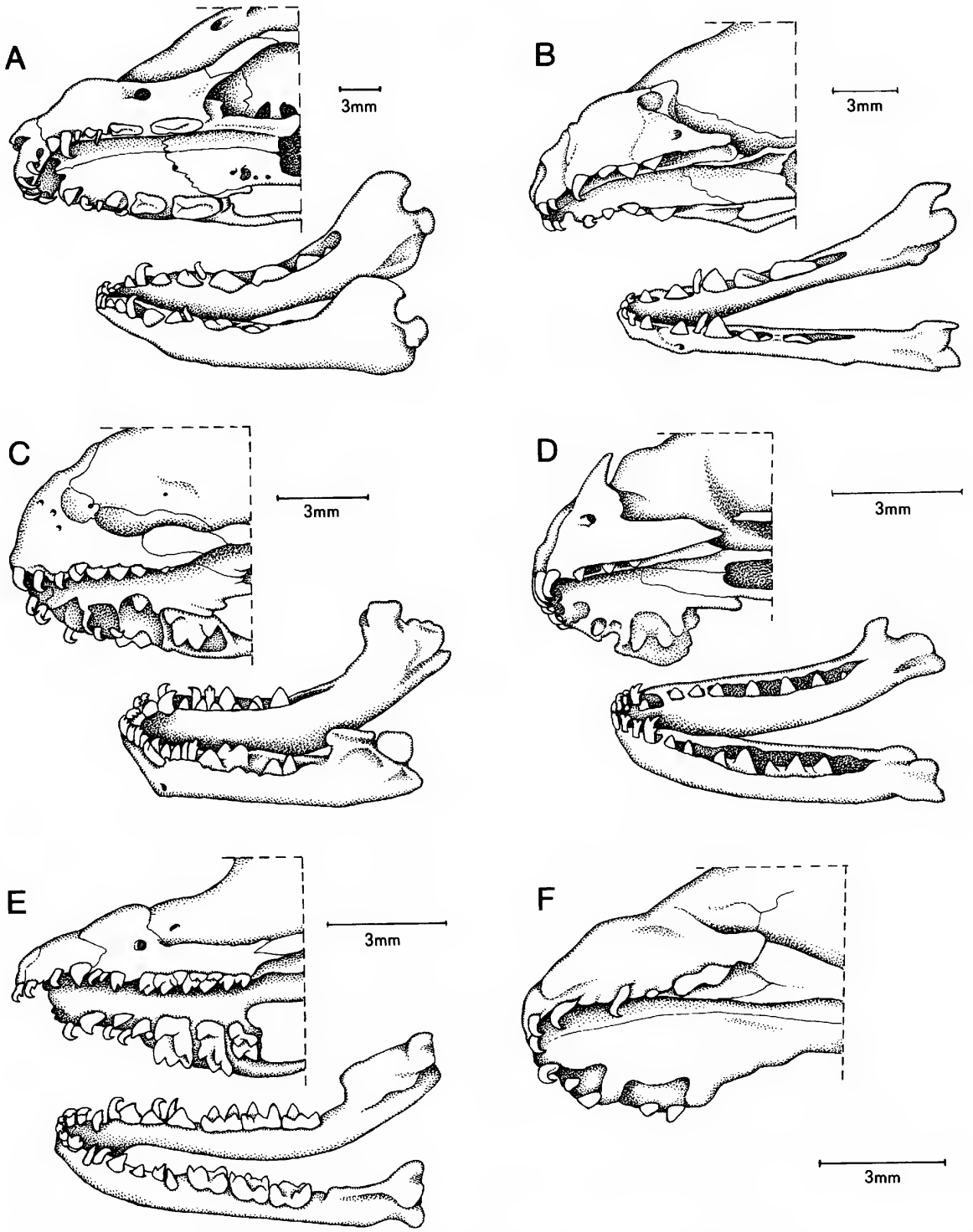

Fig. 1. Close-up views of the deciduous dentition of megachiropteran bats (A, B) and microchiropterans bats (C–F); see text for discussion. **A.** *Pteropus gouldi* (Pteropodidae, Pteropodinae; USNM 284137). **B.** *Eonycteris spelaea* (Pteropodidae, Macroglossinae; USNM 294809). **C.** *Lasiurus cinereus* (Vespertilionidae; USNM 209475). **D.** *Tadarida mexicana* (Molossidae; USNM 147786). **E.** *Thyroptera discifera* (Thyropteridae; USNM 143784). **F.** *Carollia perspicillata* (Phyllostomidae; AMNH 131770).

ina occurred independently in this taxon. Relative reduction in the size of the fused incisive foramina and consideration of the presumed phylogenetic relationships among primates (Martin, 1990) similarly suggest that the condition in *Homo* and *Pongo* is not homologous with that seen in bats. Accordingly, the condition seen in bats—fusion of the incisive foramina and concomitant reduction of the palatal process of the premaxilla—is a plausible synapomorphy of Chiroptera.

Postpalatine torus absent. The postpalatine torus is a thick, rounded lip which forms the posterior edge of the palate. This structure is found in many eutherians including all non-bat archontans (with the exception of *Loris*), insectivorans, and the putative primitive placental *Asioryctes* (Kay et al., 1992). In contrast, all bats apparently lack a postpalatine torus (Kay et al., 1992; personal obs.). The posterior edge of the palate flares ventrally in megachiropteran bats of the genus *Epomophorus,* but the bone is thin and the lip is not rounded (Anderson, 1912: fig. 36; personal obs.).

Novacek (1986: 83) suggested that "torus weak or absent" is the primitive condition for placental mammals. However, Kay et al. (1992) interpreted this character differently. As a convention in their analysis, Kay et al. (1992: 488, 496) accepted the condition seen in *Asioryctes* as primitive for all characters because this fossil taxon is believed to be "close to the ancestry of all later placental mammals." Because *Asioryctes* has a postpalatine torus, presence of this structure was interpreted as the primitive condition by Kay et al. (1992), and absence of a torus was considered to be relatively derived. If Chiroptera nests within a clade that is characterized by presence of a postpalatine torus (e.g., Archonta), this polarity assessment is probably correct with respect to bats, and absence of a torus would be parsimoniously interpreted as a derived condition diagnosing Chiroptera. The primitive condition for Eutheria as a whole remains ambiguous because marsupials and a variety of other orders lack a postpalatine torus (Novacek, 1986).

Jugal reduced and jugolacrimal contact lost. The jugal of most therian mammals is a relatively large element that forms the anteroventral rim of the orbit and contacts the lacrimal (Novacek, 1986; Wible and Novacek, 1988). This condition, which is seen in all non-bat archontans, is apparently primitive for Eutheria. In contrast, the jugal of bats is a relatively small bone confined to the middle of the zygomatic arch, separated from contact with the lacrimal by the intervening zygomatic process of the maxilla (Wible and Novacek, 1988). Reduction in the extent of the jugal and loss of a jugal-lacrimal contact is seen even in those taxa which have a well-developed postorbital process (e.g., *Pteropus*).

Reduction of the jugal is clearly a condition derived within mammals, but it is not limited to bats. The jugal is reduced (and lacimal contact lost) in erinaceomorphs, lagomorphs, and some rodents (e.g., muroids), and the jugal is entirely absent in pholidotans and soricomorphs (Carleton and Musser, 1984; Novacek, 1986; Wible and Novacek, 1988). Based on the presumed phylogenetic relationships of these taxa (Miyamoto and Goodman, 1986; Novacek, 1986, 1990, 1992a), it seems quite likely that the jugal has been independently reduced in bats, lagomorphs, pholidotans, and within Insectivora (Wible and Novacek, 1988). If bats nest within a clade characterized by an unreduced jugal (e.g., Archonta), reduction of the jugal would be parsimoniously interpreted as a synapomorphy of Chiroptera.

Two entotympanic elements in the floor of the middle-ear cavity: a large caudal element, and a small rostral element associated with the internal carotid artery. Rostral and caudal entotympanics are independent cartilages that are found in the tympanic floor and roof of many eutherian mammals (Klaauw, 1922; MacPhee and Novacek, 1993; Wible and Martin, 1993). MacPhee and Novacek (1993) recently suggested that presence of at least one such element may be primitive for Eutheria. Among eutherians, only bats, dermopterans, carnivorans, macroscelideans, and the edentate *Dasypus* have both rostral and caudal entotympanics (Klaauw, 1922; Reinbach, 1952; Hunt, 1974; MacPhee, 1981; Wible, 1984, 1993; Wible and Martin, 1993). Hyracoids have also been described as having both elements (Klaauw, 1922; Wible and Novacek, 1988), but Fischer (1989) recently reported that the caudal element is really a pro-

cess of the petrosal. Of those taxa that possess true rostral and caudal entotympanics, the internal carotid artery runs in proximity to the rostral element only in bats, dermopterans, and carnivorans (Wible, 1993; Wible and Martin, 1993). Of these forms, only bats and carnivorans have a large caudal entotympanic that forms in the posterior and posteromedial walls of the tympanic floor (Wible and Novacek, 1988; Wible, 1993; Wible and Martin, 1993).

Bat and carnivorans share a similar pattern of entotympanic morphology that includes a large caudal entotympanic and a small rostral entotympanic that is associated with the internal carotid artery (Wible, 1984; Hunt, 1974; Wible and Novacek, 1988; Wible and Martin, 1993). Because entotympanics are apparently absent in miacids (Matthew, 1909), the putative fossil sister group of Carnivora (Wyss and Flynn, 1993), it seems likely that this entotympanic pattern evolved independently in bats and carnivorans (Wible and Novacek, 1988). If so, this pattern would be interpreted as a synapomorphy of bats. However, if miacids actually had entotympanics similar to extant carnivorans (a possibility that cannot be ruled out given the uncertainties of fossil preservation), and if bats and carnivorans are closely related (a possibility suggested by some molecular data), then the entotympanic pattern described above might apply at a higher taxonomic level and would not be considered a synapomorphy of bats.

Tegmen tympani tapers to an elongate process that projects into the middle-ear cavity medial to the epitympanic recess. The tegmen tympani of bats is unique in that it is reduced and tapers to an elongate process that projects anteroventrally into the middle-ear cavity (Wible and Novacek, 1988; Wible and Martin, 1993). This condition stands in contrast to that seen in most other therians, in which the tegmen tympani lacks an elongate projecting process and instead contributes extensively to the roof or wall of the epitympanic recess (Wible and Novacek, 1988; Wible and Martin, 1993). Dermopterans resemble bats in reduction of the tegmen tympani, but the dermopteran tegmen tympani tapers to a short rather than an elongate process (Wible and Martin, 1993). The styliform tegmen tympani seen in bats is unique among mammals and can thus be interpreted as a synapomorphy of Chiroptera (Wible and Novacek, 1988).

King (1991) studied fetal specimens of *Pteropus* and claimed that megachiropterans do not exhibit the chiropteran tegmen tympani morphology described by Wible and Novacek (1988). However, this argument was refuted by Wible (1992), who demonstrated that King had incorrectly identified the tegmen tympani in skull sections (King's "tegmen tympani" was actually the alisphenoid). All bat species studied to date exhibit the unique tegmen tympani structure described above (Wible, 1992).

Proximal stapedial artery enters cranial cavity medial to the tegmen tympani; ramus inferior passes anteriorly dorsal to the tegmen tympani. The majority of eutherians exhibit a presumably primitive extracranial course for the ramus inferior of the stapedial artery (Wible, 1987, 1993; Wible and Novacek, 1988). This pattern involves origin of the ramus inferior from the proximal stapedial artery within the middle ear space, and anterior passage of the ramus inferior through the middle ear ventral to the tegmen tympani (Wible, 1987, 1993; Wible and Novacek, 1988). In contrast, bats, rodents, lagomorphs, and macroscelideans exhibit an intracranial course for this vessel (Wible, 1987, 1992; Wible and Novacek, 1988). In these taxa the ramus inferior arises from the proximal stapedial artery within the cranial cavity, and then runs forward dorsal to the tegmen tympani (Wible, 1987, 1992; Wible and Novacek, 1988). The intracranial ramus inferior of these taxa appears to be homologous to the extracranial ramus inferior of other mammals because both vessels are accompanied by the lesser petrosal nerve (Wible, 1987, 1992; Wible and Novacek, 1988). King (1991) indicated that megachiropterans lack the intracranial pattern and instead exhibited the extracranial course of the ramus inferior, but Wible (1992) demonstrated that King was misled by misidentification of the tegmen tympani. Megachiropterans and microchiropterans both exhibit a similar intracranial course for this vessel (Wible and Novacek, 1988; Wible, 1992).

Prior to giving rise to the ramus inferior,

the proximal stapedial artery enters the cranial cavity rostral to or through the tegmen tympani in rodents, lagomorphs, and macroscelideans (Wible and Novacek, 1988). In contrast, the proximal stapedial enters the cranial cavity medial to the tegmen tympani in all bats studied thus far (Wible and Novacek, 1988; Wible, 1992). This variation in morphology suggests that the intracranial course of the ramus inferior evolved independently in bats and in a clade containing rodents + lagomorphs + macroscelideans (Novacek, 1986, 1990, 1992a; Wible and Novacek, 1988). The unique condition seen in bats (proximal stapedial artery enters cranial cavity medial to tegmen tympani; ramus inferior has intracranial course) can thus be considered a synapomorphy of Chiroptera.

Postcranial Musculoskeletal System

Modification of orientation of scapular spine and shape of scapular fossae; reduction of height of spine; presence of a well-developed transverse scapular ligament. The therian scapula is characterized by presence of a longitudinal scapular spine that separates two areas of muscle attachment, the supraspinous and infraspinous fossae. In most taxa the spine originates opposite the midpoint of the glenoid fossa, and the axis of the scapular spine lies either directly in line with the axis of rotation of the head of humerus, or it is offset only a few degrees (figs. 2, 3). This condition, which is seen in marsupials, insectivorans, and non-bat archontans, is presumably primitive for eutherian mammals. In contrast, the scapular spine in all bats originates at the posterior edge of the glenoid fossa, and the long axis of the spine is offset 20–30° from the axis of rotation of the humeral head (figs. 2, 3). This condition is apparently unique among mammals.

The shift in orientation of the scapular spine in bats is correlated with changes in the shapes of fossae and the gross outline of the scapula (fig. 3). Compared with that of other mammals, the supraspinous fossa of bats has a greatly reduced anterior border and an expanded vertebral border. Because the scapular spine is relatively short, the maximum width of the infraspinous fossa occurs approximately midway along the fossa, in contrast to other mammals in which this fossa is widest at or near its distal end. Baker et al. (1991b) suggested that reduction of the supraspinous fossa and enlargement of the infraspinous fossa may be synapomorphic for bats, but changes in fossa area have yet to be demonstrated using morphometric techniques. However, the suite of shape modifications described above, including reorientation of the scapular spine, is unique to bats.

The scapular spine of most mammals is relatively deep and corresponds in height to the acromion process, with which it is continuous (fig. 2). As a result of their continuity, the scapular spine effectively braces the acromion process against forces transmitted through the clavicle. Presence of a deep scapular spine is presumably primitive for therian mammals. In contrast, the scapular spine of bats is reduced in height compared with the condition described above (fig. 2; Strickler, 1978; personal obs.). Because the scapular spine is low, the acromion process appears to be more strongly arched and less well supported in bats than in other mammals (Baker et al., 1991b). However, a well-developed ligamentous sheet known as the "transverse scapular ligament" spans the distance between the acromion process and the vertebral border of the scapula in bats (Strickler, 1978: 40). This ligament effectively braces the acromion process, apparently performing much the same function as the scapular spine in other mammals (Strickler, 1978; Altenbach, 1979). This arrangement is apparently unique to bats.

All of the features described above involve the scapular spine and are seen only in bats, so it seems likely that they represent a single character complex. This suite of modifications—reorientation of the scapular spine, modification of the shape of the scapular fossa, reduction in height of spine, and presence of a well-developed transverse scapular ligament—is an unambiguous synapomorphy of Chiroptera.

Reduction of olecranon process and humeral articular surface on ulna; presence of ulnar patella; absence of olecranon fossa on humerus. The elbow joint of bats is unique among mammals in that the ulna has a small olecranon process with a greatly reduced humeral articular surface, and the humerus lacks an olecranon fossa (Wible and Novacek, 1988;

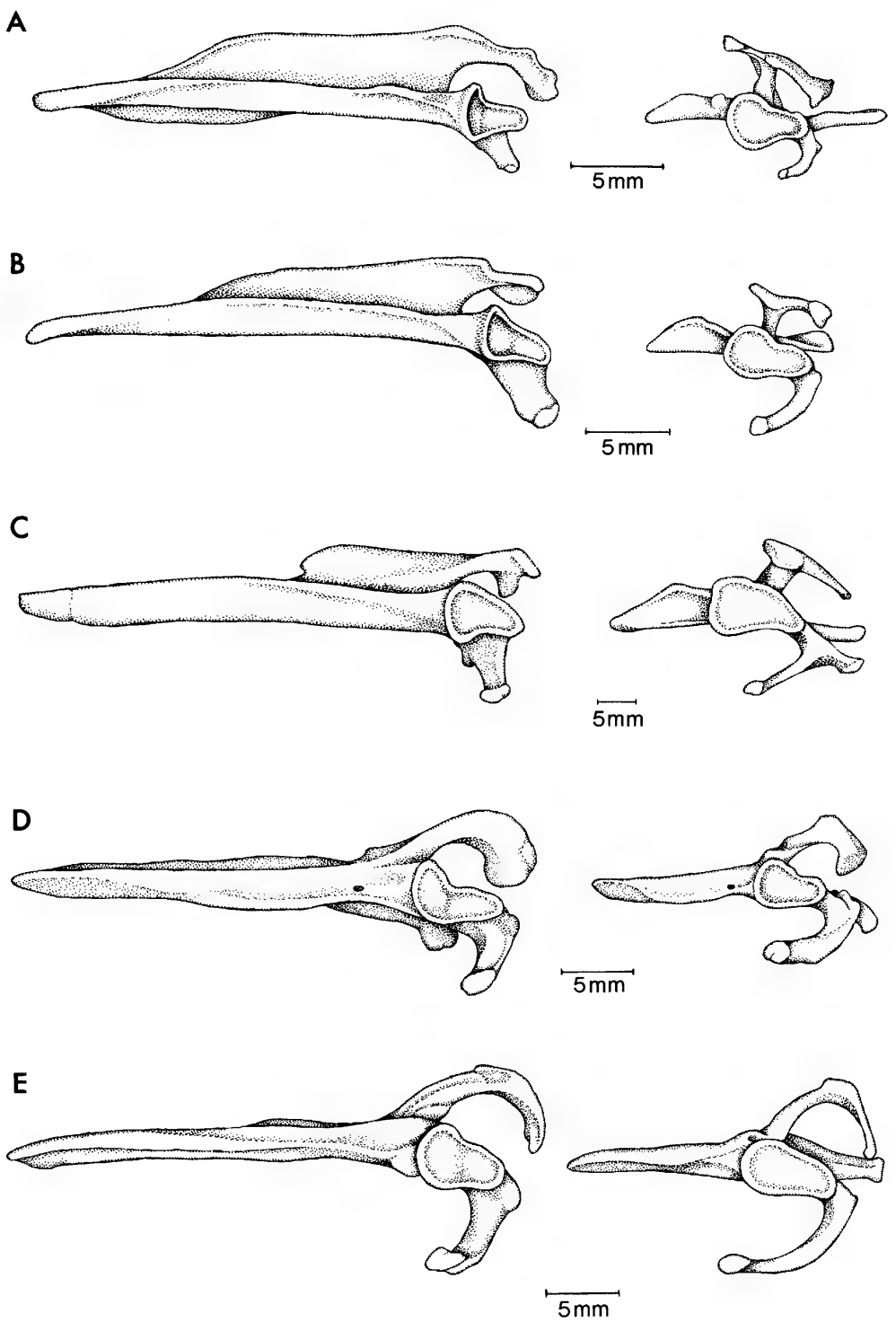

Fig. 2. Two views of the right scapula of selected archontan mammals; see text for discussion. The figures on the left provide an axillary view of the scapula with an oblique view of the glenoid fossa; the glenoid fossa directly faces the viewer in the figures on the right. **A.** *Tupaia glis* (Scandentia; USNM 396664). **B.** *Lepilemur mustelinus* (Primates; AMNH 170557). **C.** *Cynocephalus* sp. (Dermoptera; AMNH 14021). **D.** *Dobsonia crenulatum* (Megachiroptera; USNM 543180). **E.** *Vampyrum spectrum* (Microchiroptera; AMNH 261379).

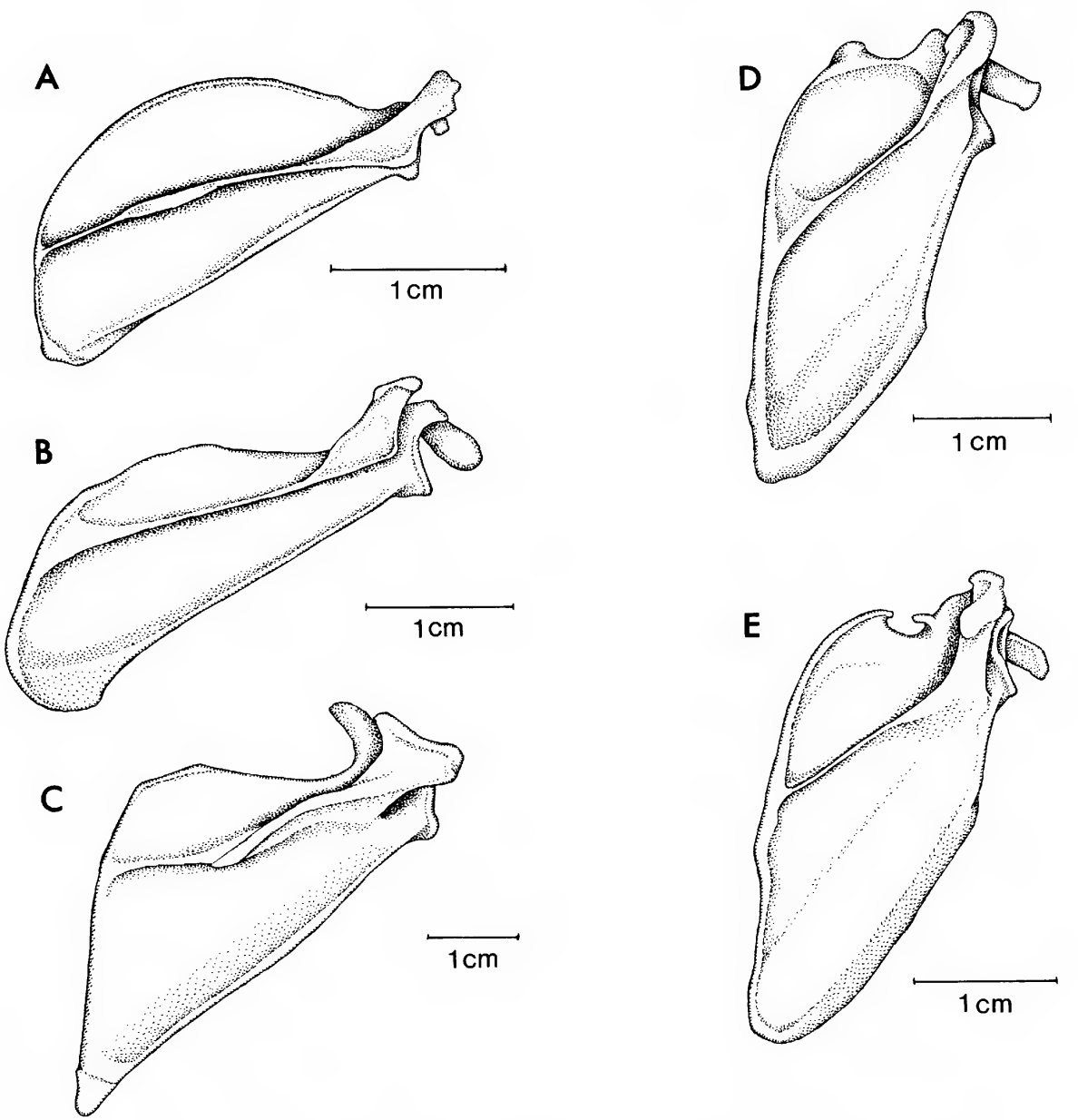

Fig. 3. Dorsal view of the right scapula of selected archontan mammals; see text for discussion. **A.** *Tupaia glis* (Scandentia; USNM 396664). **B.** *Lepilemur mustelinus* (Primates; AMNH 170557). **C.** *Cynocephalus* sp. (Dermoptera; AMNH 14021). **D.** *Dobsonia crenulatum* (Megachiroptera; USNM 543180). **E.** *Vampyrum spectrum* (Microchiroptera; AMNH 261379).

Szalay and Lucas, 1993; personal obs.). All living bats also apparently possess an "ulnar patella," an ossification in the tendon of m. triceps that articulates with the humeral trochlea when the elbow is flexed, and rides over the posterodistal surface of the humerus in a shallow groove as the elbow is extended (Walton and Walton, 1970; Szalay and Lucas, 1993; personal obs.). The shallow groove for the ulnar patella lies in the area occupied by the

olecranon fossa in other mammals. The ulnar patella, which is unique among mammals, is apparently absent in some well-preserved fossil Eocene microchiropterans (e.g., *Icaronycteris*; Jepsen, 1966; Szalay and Lucas, 1993). Despite this observation, the singular morphology of the ulnar patella suggests that this element is homologous in megachiropterans and microchiropterans and thus should have been present in the common ancestor of bats. Reduction of the olecranon process, reduction of the humeral articular surface of the ulna, loss of the olecranon fossa in the humerus, and perhaps presence of an ulnar patella and patellar groove characterize a unique suite of elbow modifications that is a synapomorphy of bats.

Extant cetaceans also exhibit reduction of the olecranon process and loss of the olecranon fossa. However, there is little reduction in area of the humeroulnar articulation, and reductions in the olecranon process and fossa are correlated with lateral compression of the long bones and development of a transverse ridge on the humerus that restricts movement in the anteroposterior plane (Barnes and Mitchell, 1978; personal obs.). Early Tertiary archaeocete whales retained a moderately large olecranon process, and the elbow joint was apparently capable of anteroposterior movement (Kellogg, 1936; Barnes and Mitchell, 1978). In this context, it seems most likely that the elbow modifications seen in cetaceans evolved independently of those seen in bats. Morphology of the cetacean elbow joint bears little resemblance to that seen in bats, and there is no reason to believe that bats and whales share any derived, homologous modifications of the elbow.

Absence of supinator ridge on humerus. The supinator ridge is a thin, prominent ridge that runs up the shaft of the humerus from the lateral epicondyle, providing a wide surface of origin for the supinator muscles of the forearm (Flower, 1885). A supinator ridge was present primitively in mammals and has been retained in most noncursorial eutherian lineages, including non-bat archontans (Flower, 1885; Wible and Novacek, 1988). In many rodents and cursorial mammals the supinator ridge is poorly developed, but the distal end of the ridge is still visible at the lateral epicondyle. The supinator ridge is apparently entirely absent only in bats, cetaceans, lagomorphs, and some rodents (e.g., *Dasyprocta*). Consideration of the probable phylogenetic relationships of these taxa (Miyamoto and Goodman, 1986; Novacek, 1986, 1990, 1992a) suggests that absence of a supinator ridge evolved independently in each of these groups. In this context, absence of the supinator ridge can be interpreted as a synapomorphy of bats.

Absence of entepicondylar foramen in humerus. The entepicondylar foramen (=supracondylar foramen) is a foramen in the distal humerus that communicates the median nerve and brachial artery (Flower, 1885). Although presence of this foramen appears to be primitive for mammals, it is absent in a variety of eutherian lineages. For example, the entepicondylar foramen is present in most insectivorans but absent in erinaceids, and is present in many carnivorans but absent in canids, ursids, and hyaenids (Flower, 1885). Among archontan mammals, the entepicondylar foramen is present in dermopterans, lemuriformes, tarsiers, and most cebids, but is absent in other anthropoids and scandentians (Flower, 1885; personal obs.). The entepicondylar foramen is uniformly absent in bats (Wible and Novacek, 1988; personal obs.). If bats are closely related to dermopterans and primates, absence of the foramen may represent a synapomorphy of bats (Wible and Novacek, 1988). However, variability of this feature within Eutheria suggests that it may not be a particularly useful character at higher taxonomic levels.

Occipitopollicalis muscle and cephalic vein present in leading edge of propatagium. Propatagial muscles are present only in gliding or flying mammals. In gliding squirrels and dermopterans, the propatagial complex consists of overlapping sheetlike muscles that extend from the side of the lower jaw to the forearm and thumb (Thewissen and Babcock, 1991, 1993; Gray and Sokoloff, 1992). The cephalic vein does not accompany the propatagial muscles into the propatagium in these taxa (Thewissen and Babcock, 1993). In contrast, the propatagial muscle in bats (m. occipitopollicalis) is a long, narrow muscle which originates from the occipital region of the skull and inserts on the base of the pollex and second metacarpal. Tendinous or mus-

cular slips may also originate on the face and in the fascia covering the pectoral muscles, and tendinous or elastic regions may intervene between muscle bellies (Mori, 1960; Stickler, 1978; Thewissen and Babcock, 1991, 1993). The cephalic vein accompanies m. occipitopollicalis into the propatagium in all bats studied to date (Thewissen and Babcock, 1993).

Layers of the sheetlike propatagial muscles in dermopterans are served by different nerves, one receiving innervation from cranial nerve VII (CN VII) and the other receiving innervation from cervical spinal nerves (Thewissen and Babcock, 1991, 1993). In contrast, individual muscle bellies in the occipitopollicalis complex receive unusual dual innervation from both CN VII and cervical spinal nerves in at least two megachiropterans (*Pteropus* and *Haplonycteris*) and two microchiropterans (*Myotis* and *Rhinopoma*; Thewissen and Babcock, 1991, 1993). At least one microchiropteran (*Tadarida*) lacks innervation from the cervical nerves, but consideration of phylogenetic relationships of the genera in question suggests that this condition is derived within Microchiroptera (Thewissen and Babcock, 1991, 1993). Dual innervation of the propatagial muscle is apparently primitive for both Megachiroptera and Microchiroptera.

The propatagial muscle in flying squirrels (*Glaucomys*) has recently been reported to receive dual innervation like that of bats (Gray and Sokoloff, 1992). However, Thewissen and Babcock (1993) noted that in flying squirrels the muscle slips innervated by CN VII are restricted to the face and do not extend into the propatagium. The dual innervation seen in individual muscle bellies of m. occipitopollicalis is a pattern unique to bats (Thewissen and Babcock, 1993). Dual innervation, an occipital origin, and a close association between m. occipitopollicalis and the cephalic vein suggest that the propatagial muscle complex of bats is uniquely derived within mammals (Thewissen and Babcock, 1991, 1993). Presence of m. occipitopollicalis in the propatagium (accompanied by the cephalic vein) thus represents a synapomorphy of Chiroptera.

Digits II-V of forelimb elongated with complex carpometacarpal and intermetacarpal joints, support enlarged interdigital flight membranes (patagia); digits III-V lack claws. The length of the digits of the hand (including metacarpals and phalanges) are less than or equal to the length of the forearm in most mammals, including all cursorial forms. Each digit in the hand is typically tipped with a claw or homologous structure (nail or hoof). The primitive condition for both the manus and pes of mammals consists of five relatively short, clawed digits with a phalangeal formula of 2–3–3–3–3 (Flower, 1885; Carroll, 1988). This pattern is retained in edentates, insectivorans, non-bat archontans, and most other nonungulate eutherians (Flower, 1885; personal obs.).

In contrast to other mammals, digits III–V of bats (and sometimes digit II) are markedly longer than the forearm, a specialization that facilitates support of greatly enlarged interdigital patagia (Wible and Novacek, 1988; personal obs.). Elongation of the digits in bats is accomplished through elongation of the metacarpals and the proximal two phalanges. The distal (third) phalanx on digits II–V is often tiny or absent in chiropterans, although the Eocene bat *Icaronycteris* has a complete phalangeal formula of 2–3–3–3–3 (Novacek, 1987). Claws are always absent on digits III–V of bats, and are frequently absent on digit II as well (Jepsen, 1966; Novacek, 1987; Wible and Novacek, 1988). Loss of claws and elongation of the digits of the forelimb, associated with presence of large interdigital patagia, represent a suite of forelimb modifications that is unique to bats among mammals.

Dermopterans, the only other mammals that have interdigital patagia, have claws on all digits of the manus and do not exhibit marked elongation of the digits (Wible and Novacek, 1988; personal obs.). In dermopterans the medial (second) phalanges are elongated relative to the proximal (first) phalanges in digits II–V (Beard, 1990, 1993a), but this modification falls far short of what is seen in bats. Even if presence of interdigital patagia is not a synapomorphy of bats (which would be the case if Chiroptera and Dermoptera are sister taxa), the relative proportions of the digits and large size of the interdigital patagia are clearly unique to bats.

In most mammals, the proximal metacar-

pals articulate with each other and with the distal carpal elements in such a way as to preclude complex movements of the metacarpals. Carpometacarpal joints are simple, allowing only flexion and extension (Flower, 1885; personal obs.). Strong metacarpal ligaments bind the proximal metacarpals to one another and hinder mediolateral (adduction/abduction), rotative, and independent movements of these elements. When present, facets associated with intermetacarpal joints are simple and facilitate only limited flexion and extension. This apparently represents the primitive condition for mammals.

Bats are unique among mammals in having complex carpometacarpal and intermetacarpal joints (Vaughan, 1959; personal obs.). Each metacarpal has a unique set of proximal facets for articulation with various convex and concave surfaces on the distal carpals, and metacarpals II–V have extensive complex facets for articulation with one another (Altenbach, 1979; personal obs.). This suite of carpometacarpal and intermetacarpal articulations permits extensive mediolateral movements of the metacarpals (adduction/abduction) but prevents anteroposterior movements. These modifications apparently brace the wing against the forces of the airstream and facilitate control of the shape and camber of the interdigital patagia during flight (Altenbach, 1979).

The suite of modifications described above—elongations of the digits, loss of claws, presence of interdigital patagia, and presence of a highly derived complex of carpometacarpal and intermetacarpal articulations—is unique to bats and therefore represents a synapomorphy of Chiroptera. Cetaceans lack claws and exhibit elongation of some digits (usually II–III or I–IV), but digit elongation is accomplished by addition of extra phalanges to the digits rather than elongation of the metacarpals and proximal phalanges, and complex carpometacarpal and intermetacarpal articulations are lacking. There is no reason to suspect that any of the forelimb modifications of cetaceans and bats are homologous.

90° rotation of hindlimbs effected by reorientation of acetabulum and shaft of femur; neck of femur reduced; ischium tilted dorsolaterally; anterior pubes widely flared and pubic spine present; absence of m. obturator internus. The acetabulum in most mammals (including monotremes and marsupials) is oriented so that the axis of rotation of the femur projects ventrolaterally from the hip (fig. 4C). The shaft of the femur is markedly offset from the femoral head and neck, which are in line with the axis of rotation. The combined effect assures that the shaft of the femur projects ventrally and slightly laterally, keeping the knee well below the level of the sacrum during most normal movements.

In contrast to the typical mammalian pattern, the femur of bats projects laterally and slightly ventrally from the hip joint, and the knee lies on or above the level of the sacrum (fig. 4A, B). This represents an approximate 90° rotation in the orientation of the hindlimb (Wible and Novacek, 1988). This effect has been produced by a pair of major modifications: reorientation of the acetabulum to face dorsolaterally rather than ventrolaterally, and reorientation of the shaft of the femur so that it lies approximately in line with the axis of rotation of the hip joint (and the head and neck of the femur) rather than being markedly offset from this axis. These modifications have been accompanied by other changes, including a dorsolateral tilting of the ischium, flaring of the anterior pubes (associated with reorientation of the acetabulum), and reduction in the neck of the femur (associated with reorientation of the shaft relative to the head of the femur). This suite of modifications is unique among mammals.

M. obturator internus is a hip muscle which originates from the inner surface of the obturator membrane and the bony rim of the obturator foramen, passes out of the pelvic cavity dorsally, and then turns laterad to insert on the greaeter trochanter of the femur. This muscle is present in the majority of mammals including marsupials, insectivorans, and non-bat archontans, but it is absent in all bats studied to date (Humphry, 1869; Coues, 1872; MacAlister, 1872; Leche, 1886; Le Gros Clark, 1924, 1926; Howell and Straus, 1933; Reed, 1951; Vaughan, 1959, 1970b). Absence of m. obturator internus seems to be functionally related to the pelvic modifications noted above, as the tilting of the ischium and flaring of the pubes have apparently reoriented the site of origin of this

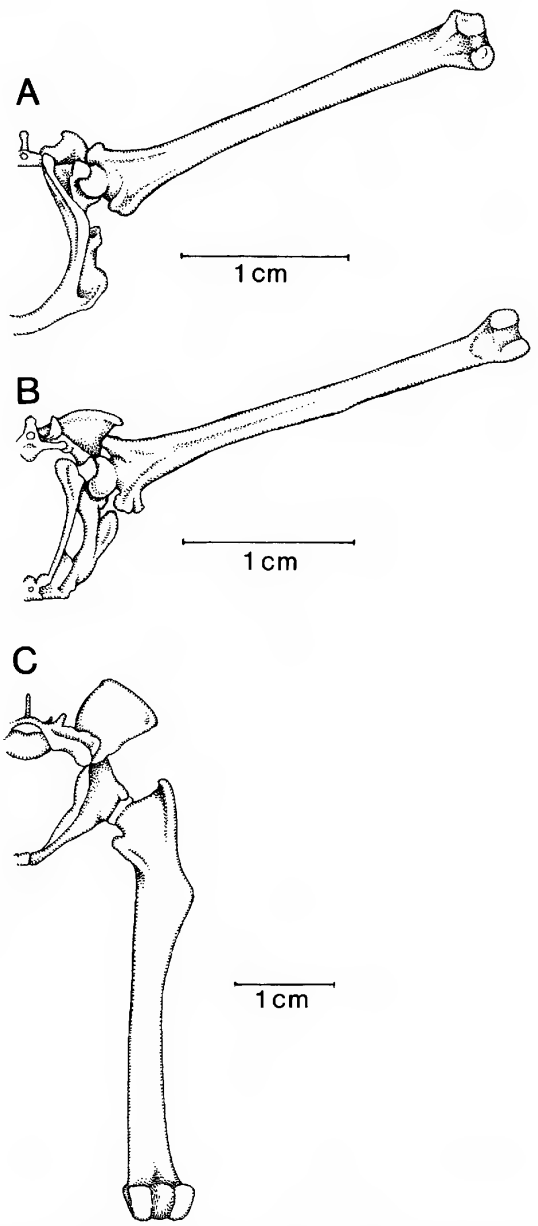

Fig. 4. Posterior view of the right half of the pelvis and articulated femur of two bats (A, B) and a scansorial quadruped (C); see text for discussion. **A.** *Rousettus amplexicaudatus* (Megachiroptera; USNM 278616). **B.** *Eumops perotis* (Microchiroptera; AMNH 15751). **C.** *Tupaia glis* (Scandentia; USNM 396664).

muscle so as to prevent effective function of the muscle. If m. obturator internus had been retained in bats, the muscle would have to pass dorsomedially almost parallel to the surface of origin, and then negotiate an acute lateral turn of at least 130° before inserting on the femur. Modifications of the pelvis associated with reorientation of the hindlimb may thus have precluded retention of this muscle.

M. psoas minor is a pelvic muscle that originates on the lumbar vertebrae and inserts on the anterior ramus of the pelvis. In most mammals, this muscle inserts on a small projection known as the iliopectineal process, which is typically located either on the ilium or at the iliopubic junction (Coues, 1872; Leche, 1886; Le Gros Clark, 1924, 1926; Howell and Straus, 1933; Reed, 1951; personal obs.). In bats, however, the insertion of m. psoas minor has shifted ventrally so that it lies entirely on the pubis, well below the level of the acetabulum (Humphry, 1869; MacAlister, 1872; Vaughan, 1959, 1970b). The projection on which the muscle inserts has also become elongated to form a structure known as the "pubic spine" (fig. 5; Vaughan, 1959; Szalay and Lucas, 1993). Some other mammals (e.g., desman talpine insectivorans) have an enlarged iliopectineal process, but in no other group does m. psoas minor insert on an elongated process of the pubis. The change in location of insertion of m. psoas minor (and development of a pubic spine) is probably functionally associated with reorientation of the acetabulum and flaring of the anterior pubes, conditions that are related to the 90° rotation in position of the hindlimbs.

The morphological features described above—90° rotation of hindlimbs effected by reorientation of the acetabulum and shaft of the femur, reduction of the neck of the femur, dorsolateral tilting of the ischium, flaring of the anterior pubes, presence of a pubic spine, and absence of m. obturator internus—appear to be functionally related and thus seem to represent a single character complex. This complex is unique to bats among mammals.

Absence of m. gluteus minimus. This muscle originates from the illium and inserts on the greater trochanter of the femur, which it abducts and rotates. M. gluteus minimus is present in most mammals, including monotremes, marsupials, and non-bat archontans (Coues, 1872; Leche, 1886; Le Gros Clark, 1924, 1926; Howell and Straus, 1933; Ellsworth, 1974). In contrast, m. gluteus mini-

mus is absent in insectivorans and bats (Humphry, 1869; MacAlister, 1872; Reed, 1951; Vaughan, 1959, 1970b). If bats nest within a clade characterized by presence of m. gluteus minimus (e.g., Archonta), absence of this muscle may be interpreted as a synapomorphy of bats. This would not be true if bats are closely related to insectivorans.

It should be noted that absence of m. gluteus minimus may well represent another feature functionally linked with the suite of hip modifications described above (i.e., those associated with reorientation of the hindlimb). However, this cannot be assumed a priori because absence of m. gluteus minimus, unlike the other features, is not unique to bats.

Absence of m. sartorius. This muscle originates from the ilium and/or inguinal ligament and inserts on the medial aspect of the tibia. M. sartorius is present in monotremes, marsupials, and most eutherians, including erinaceid insectivorans and non-bat archontans (Coues, 1872; Leche, 1886; Le Gros Clark, 1924, 1926; Howell and Straus, 1933; Reed, 1951; Ellsworth, 1974). Presence of this muscle thus appears to be the primitive condition for mammals.

M. sartorius is absent in bats, macroscelideans, and soricid and talpid insectivorans (Humphry, 1869; MacAlister, 1872; Leche, 1886; Reed, 1951; Vaughan, 1959, 1970b; Wible and Novacek, 1988). Absence of this muscle in some (but not all) insectivorans suggests that m. sartorius has been lost within insectivorans, and it has probably also been lost independently in bats and macroscelideans. If bats nest within a clade characterized by presence of m. sartorius (e.g., Archonta), then absence of this muscle would be interpreted as a synapomorphy of Chiroptera. This might not be true if bats are closely related to macroscelideans or insectivorans.

Vastus muscle complex not differentiated. The vastus complex comprises a set of muscles that originate on the proximal femur and insert into the patella and patellar ligament. These muscles apparently originate from a single mass which differentiates into several muscles during development. Five distinct vastus muscles are seen in monotremes; three are found in most eutherians (e.g., insectivorans, scandentians, primates), and two are present in some taxa (e.g., marsupials, dermopterans; Coues, 1872; Leche, 1886; Le Gros Clark, 1924, 1926; Howell and Straus, 1933; Reed, 1951; Ellsworth, 1974). In contrast, the vastus in bats consists of a single, undifferentiated muscle mass (Humphry, 1869; MacAlister, 1872; Leche, 1886; Reed, 1951; Vaughan, 1959, 1970b). This unique condition is apparently derived within mammals.

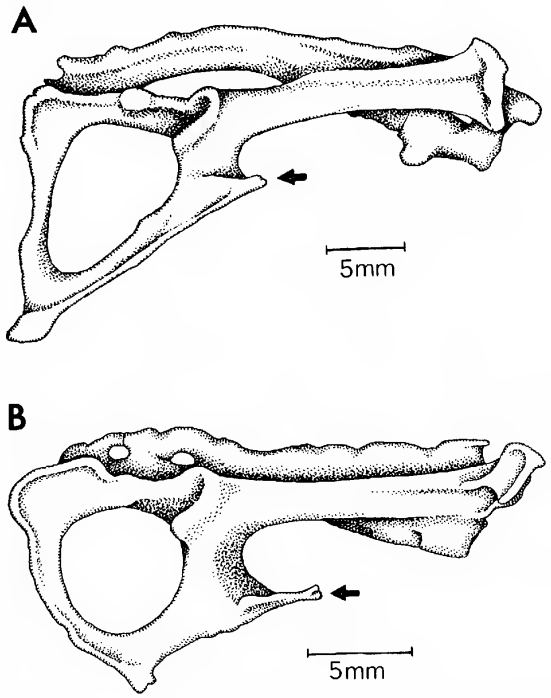

Fig. 5. Lateral view of the right side of the pelvis of a megachiropteran bat (A) and microchiropteran bat (B); see text for discussion. Arrows indicate the location of the pubic spine, the insertion site of the psoas minor muscle. **A.** *Dobsonia crenulata* (USNM 543180). **B.** *Vampyrum spectrum* (AMNH 261379).

Like other muscular modifications noted above, lack of differentiation of the vastus muscle complex may be functionally associated with reorientation of the hindlimb. However, this cannot be assumed a priori because the number of differentiated muscles in the vastus complex may have been reduced in other mammalian groups (e.g., marsupials, dermopterans) for reasons unrelated to hip reorganization. Interpretation of transformations of this character in the basal branch-

es of Mammalia is ambiguous, but it seems clear that a completely undifferentiated vastus is unique to bats.

Reorientation of upper ankle joint facets on calcaneum and astragalus; trochlea of astragalus convex, lacks medial and lateral guiding ridges; tuber of calcaneum projects in plantolateral direction away from ankle and foot; peroneal process absent; sustentacular process of calcaneum reduced, calcaneoastragalar and sustentacular facets on calcaneum and astragalus coalesced; absence of groove on astragalus for tendon of m. flexor digitorum fibularis. The upper ankle joint in mammals is formed by a series of articulations between the distal tibia and fibula and the astragalus and calcaneum. Primitively, the eutherian tibia articules with the astragalus, and the fibula articulates with both the astragalus and calcaneum (Szalay, 1977, 1984, 1993; Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Szalay and Lucas, 1993). The proximal articular surfaces of the astragalus collectively form an "astragalar trochlea," which is typically saddle-shaped and bounded by medial and lateral guiding ridges. The tibial and fibular facets on the astragalar trochlea and on the calcaneum lie in planes that are oblique to the distal facets for the cuboid and navicular, and the axis of the tuber of the calcaneum (which projects in a posterior direction away from the ankle and foot) passes through the cuboid facet (Szalay, 1977, 1984, 1993; Szalay and Decker, 1974; Szalay and Drawhorn, 1980; Szalay and Lucas, 1993; personal obs.). This arrangement constrains extension at the upper ankle joint because the tuber of the calcaneum limits movement of the tarsus relative to the tibia and fibula.

Bats have a unique upper ankle joint which permits almost full extension of the foot. The trochlea of the astragalus lies in a plane parallel to that of the navicular facet. The trochlear surface is smoothly convex and lacks medial and lateral guiding ridges (Wible and Novacek, 1988; personal obs.). The fibular facet on the calcaneum (when present) has shifted its position to the lateral side of the base of the calcaneal tuber, and in many forms the plane of the fibular facet lies parallel to that of the cuboid facet. The calcaneal tuber, rather than projecting in a posterior direction away from the foot, is directed plantolaterally. As a result, the axis of the calcaneal tuber no longer intersects the cuboid facet, but rather passes through the anterior surface of the body of the calcaneum. When the foot is extended, the calcaneal tuber does not interfere with movement at the upper ankle joint. This suite of modifications is unique to bats among therian mammals.

The peroneal process of the calcaneum, under which the tendon of m. peroneus longus passes, projects laterally from the body of the calcaneum in most mammals. The primitive therian calcaneum was apparently characterized by a prominent peroneal process, but the process has been reduced or lost in a variety of lineages including bats, tupaiine scandentians, and extant euprimates (Szalay, 1977, 1982, 1984; Szalay and Decker, 1974; Novacek, 1980; Szalay and Drawhorn, 1980; Wible and Novacek, 1988; Szalay and Lucas, 1993). Because ptilocercine scandentians and some Paleogene euprimates have a distinct peroneal process, Wible and Novacek (1988) suggested that this structure was lost independently in bats, tupaiines, and within euprimates. Independent loss in bats seems particularly likely when reorientation of the calcaneal tuber is taken into account. The plantolateral orientation of the chiropteran calcaneal tuber is unique, and this arrangement effectively precludes presence of a peroneal process (the normal location for the mammalian peroneal process is occupied by the base of the calcaneal tuber in bats).

The lower ankle joint of mammals comprises the joint between the calcaneum and astragalus. Typically, two distinct points of articulation are involved: a lateral calcaneoastragalar articulation, and a medial sustentacular articulation (Szalay and Decker, 1974; Szalay, 1977, 1982; Szalay and Lucas, 1993). The sustentacular facet on the calcaneum is located on the sustentacular process, a shelflike medial projection from the body of the calcaneum; the calcaneoastragalar facet is located on the body itself. The facets for these two articulations are separate in marsupials, insectivorans, non-bat archontans, and the majority of therian mammals (Szalay and Decker, 1974; Szalay, 1977, 1982; Szalay and Lucas, 1993; personal obs.). This presumably represents the primitive condition for Theria.

Bats are unique in that the sustentacular process has been reduced and the calcaneoastragalar and sustentacular facets are continuous on the medial side of the body of the calcaneum (Szalay and Lucas, 1993; personal obs.). Wible and Novacek (1988: table 3) noted that bats have the "calcaneal-astragalar facet of the calcaneum modified from convex process to depression or trough." This appears to be a somewhat misleading description of the same modification: the "depression" or "trough" is actually formed by coalescence of the two facets, which lie in slightly different planes and form a concave articular facet when fused. Similarly, Beard (1993a) stated that the sustentacular facet is greatly reduced or absent in bats, an impression that follows from identification of the coalesced facets as the calcaneoastragalar facet. Reduction of the sustentacular process contributes to the impression that the sustentacular facet is absent in bats.

M. flexor digitorum fibularis (=m. flexor hallucis longus) originates from the posterodistal surface of the fibula and the interosseous membrane, passes across the ankle medial to the calcaneum, and inserts into the ventral surfaces of the distal phalanges (Reed, 1951; Vaughan, 1959). There is a groove for the tendon of this muscle on the posterior surface of the astragalus in the majority of mammals, including all non-bat archontans, and presence of this groove is presumably primitive for mammals (Beard, 1993a). Rearrangement of the upper and lower ankle joints in bats has apparently resulted in a somewhat different location for the tendon of m. flexor digitorum fibularis. In bats, this tendon apparently passes over the surface of the calcaneum medial to the deflected calcaneal tuber (Vaughan, 1970b). Accordingly, a groove for the tendon of m. flexor digitorum fibularis is not present on the astragalus of bats (Beard, 1993a), a condition that is apparently unique to bats among therians.

The morphological features described above—reorientation of upper ankle joint facets on calcaneum and astragalus, a convex astragalar trochlea lacking medial and lateral guiding ridges, projection of the tuber of calcaneum in a plantolateral direction, absence of the peroneal process, reduction of the sustentacular process of calcaneum, coalescence of the calcaneoastragalar and sustentacular facets on calcaneum and astragalus, and absence of groove on astragalus for tendon of m. flexor digitorum fibularis—appear to be functionally related and thus seem to represent a single character complex. This complex is unique to bats among mammals.

Presence of calcar and depressor ossis styliformes muscle. The calcar, a cartilaginous and/or osseous element that extends from the calcaneum to support the trailing edge of the uropatagium, is a structure unique to bats. M. depressor ossis styliformes, the muscle that controls the position of the calcar relative to the tibia and ankle, is also unique. A calcar is absent in one pteropodid (*Sphaerias*), *Craseonycteris, Rhinopoma,* a few phyllostomid species, and several Eocene microchiropterans (including *Icaronycteris*), but all other bats (including *Palaeochiropteryx*) have a calcar (Anderson, 1912; Jepsen, 1966; Walton and Walton, 1970; Smith, 1980; Habersetzer and Storch, 1987). Although m. depressor ossis styliformes has been studied in only a few taxa, it appears similar in morphology in both megachiropterans and microchiropterans (Mori, 1960; Vaughan, 1959, 1970b; personal obs.). On the basis of presumed phylogenetic relationships among the genera and families in question (Anderson, 1912; Van Valen, 1979; Smith, 1980; Pierson, 1986; Novacek, 1987), it seems likely that the absence of the calcar and m. depressor ossis styliformes in some bat taxa is a secondarily derived condition. Presence of a calcar and m. depressor ossis styliformes can therefore be interpreted as a synapomorphy of bats.

Shape of distal facet on entocuneiform. The distal facet of the entocuneiform in most mammals is very narrow and includes a strong plantodistal process that interlocks with a groove on the plantar surface of the first metatarsal (Beard, 1993a). This presumably represents the primitive condition for mammals. In primates and dermopterans, the distal entocuneiform process is wide and the plantodistal process is reduced or absent, a condition that is relatively derived (Beard, 1993a). In contrast, bats have a proximodistally shortened entocuneiform with a flat, triangular distal facet (Beard, 1993a), a condition that is also derived with respect to the

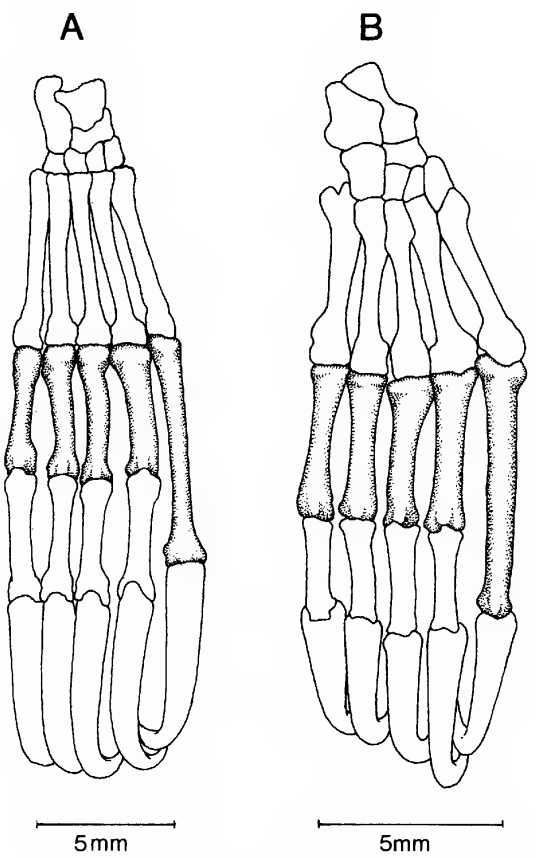

Fig. 6. Dorsal view of the foot of a megachiropteran bat (A) and microchiropteran bat (B) showing the relative proportions of the phalanges. Note that the proximal phalanx of digit I (right side of each figure) is greatly elongated relative to those of the other digits. **A.** *Rousettus amplexicaudatus* (USNM 278616). **B.** *Phyllostomus hastatus* (AMNH 266071).

primitive mammalian pattern. Interpretation of the pattern of transformation of this character depends upon perceived relationships among bats, primates, and other mammalian orders. The chiropteran condition, which is unique to bats among mammals, may represent a synapomorphy of bats.

Elongation of proximal phalanx of digit I of foot. The proximal phalanx of pedal digit I is less than or equal to the length of the proximal phalanges of the other digits in non-bat mammals. In contrast, the proximal phalanx of digit I in most bats is approximately 1.5 times longer than the proximal phalanges of the othr pedal digits (fig. 7; Szalay and Lucas, 1993; personal obs.). This elongation effectively extends the length of digit I, which has only two phalanges, and brings the claw in line with those of the other pedal digits (each of which have three phalanges). Elongation of the proximal phalanx of digit I is unique to bats among mammals.

Th proximal phalanx in digit I is not elongated in three microchiropteran groups (Hipposiderinae, Thyropteridae, and Myzopodidae). This difference is correlated with a reduction of the number of phalanges in digits II–V (Walton and Walton, 1970), another condition that is clearly derived within mammals. On the basis of presumed phylogenetic relationships among the various families of bats (Van Valen, 1979; Smith, 1980; Pierson, 1986; Novacek, 1987), it seems likely that the ancestral condition for bats consisted of a phalangeal formula of 2–3–3–3–3 with the proximal phalanx of digit I elongated. By this interpretation, secondary reduction of the elongated first phalanx of digit I evolved concurrently with reduction of the phalangeal formula to 2–2–2–2–2 in some microchiropteran lineages, thus preserving the ancestral arrangement of the claws. Therefore, elongation of the proximal phalanx of digit I (which is seen in Megachiroptera and primitively in Microchiroptera) can be interpreted as a synapomorphy of bats.

Fetal Membranes

Orientation of embryonic disc at time of implantation. Implantation of the embryo in the uterus generally occurs at the bilaminar blastocyst stage of embryonic development. At the time of implantation, the embryonic disc typically exhibits one of three orientations relative to the mesentery of the uterus (mesometrium). "Mesometrial" implantation describes a condition in which the embryonic pole of the blastocyst is directed toward the mesometrium; implantation is termed "antimesometrial" when the abembryonic pole is directed toward the mesometrium (Luckett, 1975, 1977, 1980b, 1993; Mossman, 1987). "Orthomesometrial" orientation describes a condition in which an axis running through the embryonic and abembryonic poles is oriented at a 90° angle

to the mesometrium (Luckett, 1975, 1977, 1980b, 1993; Mossman, 1987). These patterns of orientation remain constant throughout early development in all non-bat placental mammals regardless of differences in the degree of invasive activity that accompanies implantation (Luckett, 1977, 1980b, 1993).

In megachiropterans and most microchiropterans, the embryonic disc does not bear a constant orientation to one pole of the uterus. Instead, the disc appears to be directed toward the tubo-uterine junction rather than bearing a specific orientation to the site of mesometrial attachment (Rasweiler, 1979; Luckett, 1980b, 1993). A few bats (vespertilionids, thyropterids, desmodontines) exhibit fixed antimesometrial implantation, but this appears to be a condition derived within Microchiroptera (Luckett, 1980, 1993). In this context, orientation of the embryonic disc toward the utero-tubal junction can be interpreted as a synapomorphy of Chiroptera (Luckett, 1980b, 1993).

Differentiation of a free, glandlike yolk sac. A free yolk sac forms early in development and is maintained as a simple, sacciform structure throughout most of gestation in the majority of mammals, including most insectivorans, dermopterans, and primates (Luckett, 1975, 1977; Mossman, 1987). This condition is presumed to be primitive for mammals (Luckett, 1977). In megachiropterans and many microchiropterans (rhinopomatids, emballonurids, rhinolophids, molossids) a free yolk sac forms (fig. 7A, B, D) but subsequently collapses to lie as a flattened sac over the surface of the definitive placental disc (Gopalakrishna, 1958; Luckett, 1980b, 1993; Rasweiler, 1990, 1992). The endodermal cells of the yolk sac become hypertrophied, and the resulting yolk sac assumes a unique "glandlike" appearance that is not seen in other mammals (fig. 7C, E, F; Gopalakrishna, 1958; Luckett, 1977, 1980b, 1993; Mossman, 1987; Wible and Novacek, 1988; Rasweiler, 1990, 1992). This complex apparently stores glycogen and lipids that serve as an energy source just before parturition (Stephans and Easterbrook, 1968; Rasweiler, 1990; Luckett, 1993). Presence of a free, glandlike yolk sac is unique to bats among mammals (Luckett, 1980b, 1993).

Microchiropterans that fail to develop as described above exhibit either of two derived conditions: (1) paedomorphic retention of an apparently absorptive bilaminar omphalopleure (e.g., phyllostomids and noctilionids), or (2) formation of a trilaminar omphalopleure without development of a free yolk sac, but with collapse and hypertrophy of the yolk sac wall (e.g., megadermatids, thyropterids, vespertilionids; Luckett, 1980b, 1993). Both of these conditions appear to be derived from a developmental pattern that involved differentiation of a free, glandlike yolk sac (Luckett, 1993). Because development of a free, glandlike yolk sac appears to be primitive for bats (and is unique to bats among mammals), development of this structure can be interpreted as a synapomorphy of Chiroptera.

Preplacenta and early chorioallantoic placenta diffuse or horseshoe-shaped, with definitive placenta reduced to a more localized discoidal structure. The eutherian preplacenta consists of a somewhat thickened layer of trophoblast which forms where the maternal epithelium of the uterus has broken down. Maternal capillaries lie in close contact with the trophoblast of the preplacenta, but no fetal vessels have yet formed within the trophoblast (Mossman, 1987). The preplacenta eventually becomes vascularized on part or all of its fetal surface by the vascular allantois, thereby establishing the definitive chorioallantoic placenta (Luckett, 1980b; Mossman, 1987).

Placental development among bats is unique in that it involves formation of a broad diffuse or horseshoe-shaped preplacenta and early chorioallantoic placenta, which is later reduced to form a more localized, discoidal definitive placenta (fig. 7; Luckett, 1980b, 1993; Rasweiler, 1990, 1992). A broad diffuse preplacenta also forms and is reduced in hyracoids, but the definitive placenta is zonary rather than discoidal (Mossman, 1987). The pattern of early placental development seen in bats occurs in no other group of mammals and thus may be considered a synapomorphy of Chiroptera (Luckett, 1980b, 1993).

Definitive chorioallantoic placenta endotheliochorial. The degree of invasive activity of the definitive chorioallantoic placenta varies widely among mammals. Three major placental types are recognized. An "epitheli-

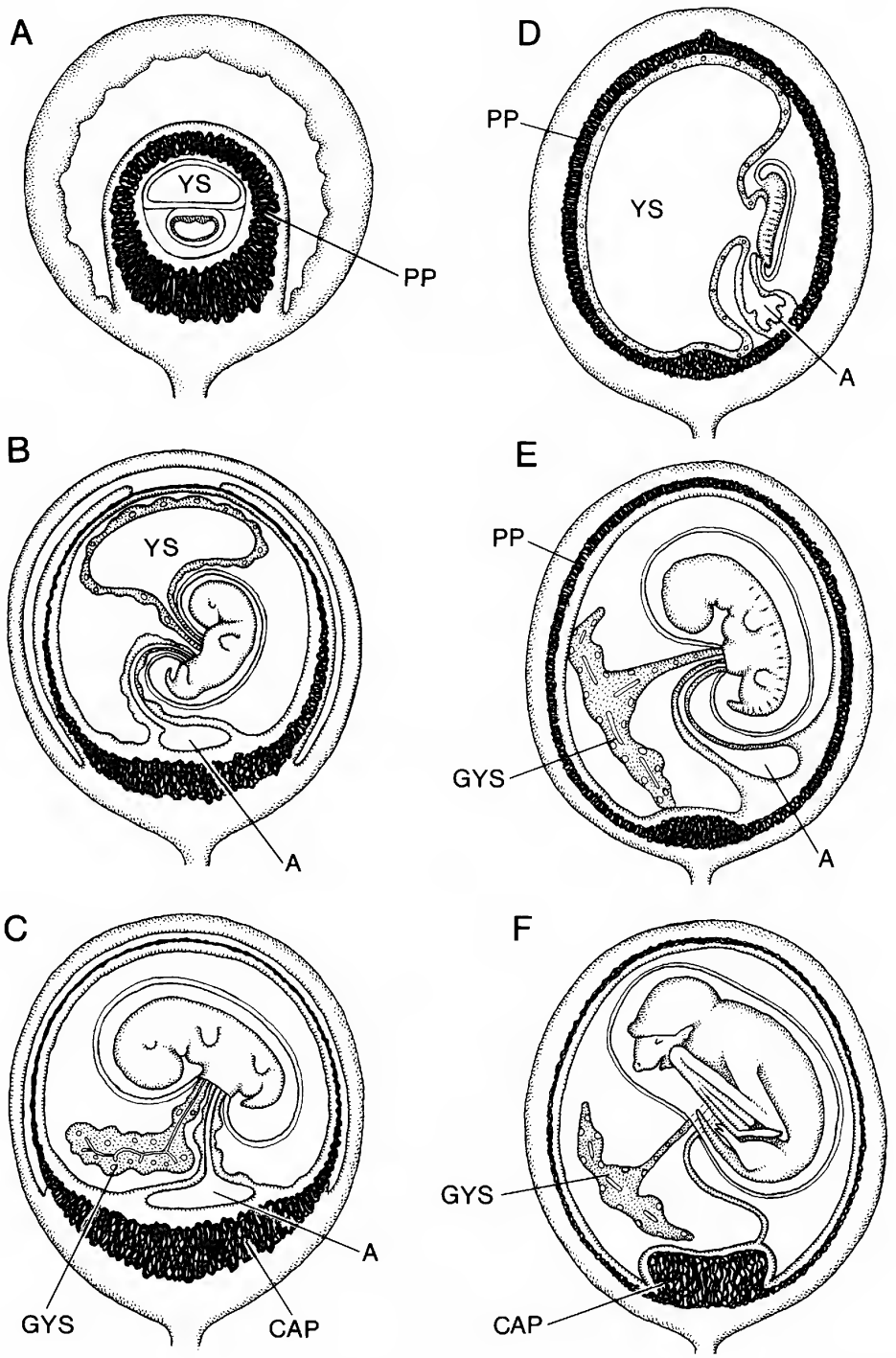

Fig. 7. Stages in fetal membrane development in a megachiropteran bat (A–C) and microchiropteran bat (D–F); see text for discussion. The developmental stages shown for the two bats are not equivalent, but simply represent progressive stages in fetal development. The different stages in each sequence (e.g., A–C) have not been drawn to relative scale. **A, B, C.** *Pteropus* sp. (redrawn from Mossman, 1987: pl. 9). **D, E, F.** *Molossus ater* (redrawn from Rasweiler, 1992: figs. 18.6, 18.7, 18.9). A = allantois; CAP = definitive chorioallantoic placenta; GYS = glandular yolk sac; PP = preplacenta; YS = yolk sac.

ochorial" placenta is one in which there is no loss of maternal tissue, so the chorionic trophoblast is effectively separated from the maternal blood supply by at least two tissue layers (Luckett, 1977; Mossman, 1987). An "endotheliochorial" placenta forms when the maternal epithelium and all or part of the underlying connective tissue are lost, resulting in apposition of the chorionic trophoblast and the maternal capillary endothelium (Luckett, 1977; Mossman, 1987). Finally, a "hemochorial" placenta is established when all of the maternal tissue separating the maternal blood from the trophoblast breaks down, bathing the trophoblast in maternal blood (Luckett, 1977; Mossman, 1987).

Two placenta types occur in bats: endotheliochorial and hemochorial. According to Luckett (1980b: 257),

> Maternal capillary endothelium persists within the placenta and is separated from the syncytiotrophoblast by a relatively thick, PAS-positive lamina ("interstitial membrane") in the morphotype of the families Pteropodidae, Rhinopomatidae, Rhinolophidae, Emballonuridae, Megadermatidae, and Noctilionidae. Both comparative and ontogenetic analyses suggest that this endotheliochorial relationship represents the primitive chiropteran condition.

Some megachiropterans and members of the remaining microchiropteran families develop a hemochorial placenta, but this appears to be a condition that is secondarily derived within bats (Luckett, 1980b, 1993). Data from an ultrastructural study of changing tissue relationships during ontogeny of the placenta in *Myotis* (Enders and Wimsatt, 1968) apparently provide evidence for the transformation of endotheliochorial to hemochorial placentation (Luckett, 1980b, 1993). In this context, it seems most likely that the primitive condition for bats is presence of an endotheliochorial placenta (Luckett, 1980b, 1993).

Among non-bat eutherians, an endotheliochorial placenta is found in some edentates (bradypodids), some insectivorans (soricids, some talpids), tubulidentates, some rodents (heteromyids), proboscideans, carnivorans, scandentians, and two species of strepsirhine primates (Luckett, 1975, 1977, 1980b, 1993; Mossman, 1937, 1987). Most strepsirhine primates have an epitheliochorial placenta, while other archontans (dermopterans, tarsiers, and anthropoids) have a hemochorial placenta (Luckett, 1975, 1977, 1980b, 1993; Mossman, 1937, 1987). Although still the source of some controversy (e.g., see Martin, 1990), it now appears that the epitheliochorial placenta is primitive for eutherian mammals and probably for Archonta and Primates as well (Luckett, 1975, 1977, 1980b, 1993; Mossman, 1987).

Luckett (1975, 1977, 1993) has argued that there is no uniform shared pattern of fetal membrane development among most taxa with an endotheliochorial placenta, and thus that endotheliochorial placentation has evolved convergently many times in mammals. Luckett (1993: 175) observed that

> . . . careful consideration of all developmental features associated with endotheliochorial placentation . . . , including fate of the polar trophoblast, amniogenesis, patterns of implantation, and fate of the definitive yolk sac, suggests that an endotheliochorial placenta has developed homologously in the chiropteran suborders, but convergently in carnivorans and scandentians.

If bats are members of Archonta, then presence of an endotheliochorial placenta would be interpreted as a synapomorphy of bats. This feature was noted as a chiropteran synapomorphy by Wible and Novacek (1988: table 3), who described it as "prominent 'interstitial membrane' in the chorioallantoic placenta." It should be noted, however, that some workers consider an endotheliochorial placenta to be primitive for eutherian mammals (e.g., Martin, 1990), while others do not believe that bats belong to a monophyletic Archonta (e.g., Stanhope et al., 1992, 1993). Under these interpretations, endotheliochorial placentation may be either ambiguous or may represent a plesiomorphic condition.

Nervous System

Cortical somatosensory representation of forelimb reverse of that in other mammals. Somatic sensory input from various parts of the body is received by specific areas of the neocortex in mammals. "Somatotopic maps"

of the primary somatosensory cortex (fig. 8) may be obtained by systematically stimulating sensors in different parts of the body and recording the pattern of electrical responses in the neocortex. These maps typically contain discrete representations of the body surface. Somatotopic maps of primary somatosensory cortex reveal a similar orientation of forelimb representation in most mammals, with the distal elements of the forelimb occurring rostral to more proximal elements in the somatotopic map (fig. 8E). This relative orientation of the forelimb representation is seen in monotremes, marsupials, and all nonbat taxa studied thus far (Bohringer and Rowe, 1977; Kaas, 1983; Wible and Novacek, 1988).

Somatotopic maps have been compiled for only three bats. In one microchiropteran (*Macroderma*) and one megachiropteran (*Pteropus*), somatosensory forelimb representations are the reverse of that of the body, which maintains the same relative position as seen in somatotopic maps of other mammals (fig. 8C, D; Calford et al., 1985; Wise et al., 1986). This arrangement is apparently unique among mammals. Pettigrew et al. (1989) stated that one microchiropteran (*Antrozous*) lacks this reversal of the forelimb representation, and cited Zook and Fowler (1982) and Zook (personal commun.) as the sources of this information. However, data supporting this claim have never been published. Contra Pettigrew et al. (1989), Zook and Fowler's (1982) publication, which is an abstract, contains no mention of forelimb orientation. Kaas (personal commun.) has seen the summary diagrams of Zook and Fowler, and reports that they show the same forelimb orientation in *Antrozous* as seen in other bats. Given the data currently available, it seems likely that reversal of the forelimb representation represents another synapomorphy of bats.

REJECTED PUTATIVE SYNAPOMORPHIES

Recognition of phylogenetic relationships and identification of synapomorphies is an iterative process, and disagreements concerning conclusions are common. Systematists are often faced with lists of putative synapomorphies that must be evaluated in terms of the observational methods employed, criteria for homology, perceived levels of within- and among-taxon variation, and the phylogenetic context in which a given feature is interpreted. There are numerous reasons why a putative synapomorphy may be validly rejected.

Perhaps the most basic reason for rejecting a synapomorphy is simple observational error, when taxa have been cited as having a feature that they do not actually exhibit, or lacking a feature that is clearly present. Putative synapomorphies in such cases may be found to apply at higher or lower taxonomic levels than originally reported, or they may be rendered ambiguous when the observational data are corrected. This can also occur when additional sampling indicates that a distribution originally inferred for a character (e.g., uniform presence in a given family or order) is incorrect. In some cases, more detailed sampling within groups may document levels of within-group variation that meet or exceed the amount of among-group variation originally perceived. This variation may result in such ambiguity that evolutionary interpretation of a character becomes impossible, leading to rejection of the feature as a phylogenetic character at the taxonomic level under consideration.

Other reasons for rejecting putative synapomorphies involve definition and homology of the features in question. Some characters have been defined in vague terms that suggest but do not support a hypothesis of homology (e.g., "derived, non-insectivorous dentition" cited by Smith and Madkour, 1980). If further comparisons or developmental data indicate that non-homologous conditions have been lumped together under such a description (as in this case; Koopman and MacIntyre, 1980), the character may be rejected on the grounds that it fails an initial test of similarity, a prerequisite for homology. Such character descriptions are, essentially, too superficial to be phylogenetically informative.

Finally, a critical component of character interpretation is the phylogenetic context. The position of a clade in the phylogenetic tree may strongly affect hypotheses of synapomorphy. For example, a particular character

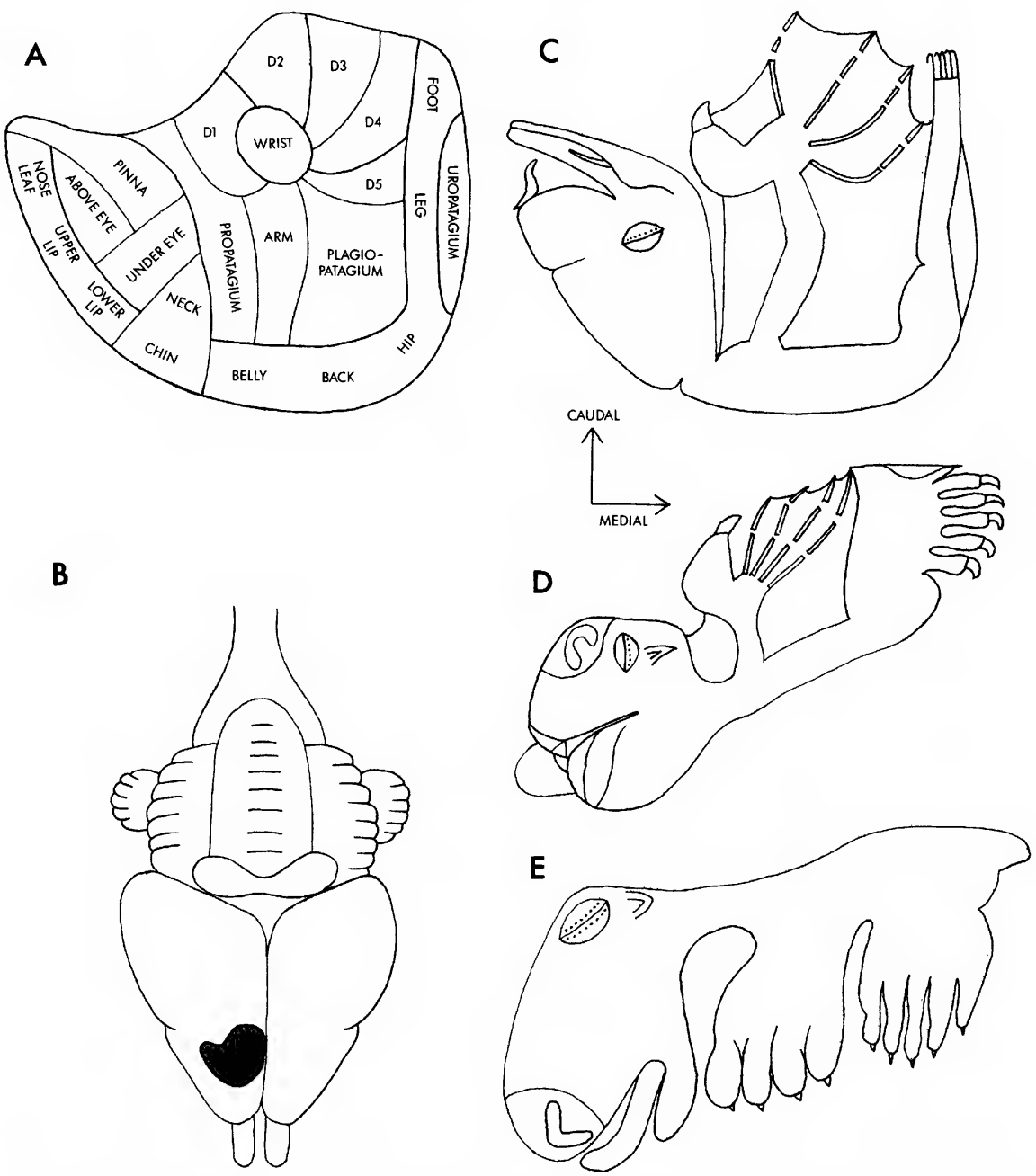

Fig. 8. Cortical representations of the body surface as determined from somatosensory mapping experiments; see text for discussion. All of the figures shown here were redrawn from Wise et al. (1986). **A.** Body surface "map" reconstructed from receptive field data collected from two specimens of the microchiropteran bat *Macroderma gigas*. **B.** Approximate location of the body surface map (A) in the brain of *Macroderma gigas*. **C.** Schematic representation (homunculus) of the body surface of *Macroderma gigas*. Compare this homunculus with the cortical map in figure A, from which it was derived. **D.** Schematic representation of the body surface of a megachiropteran bat, *Pteropus poliocephalus* (from Calford et al., 1985). **E.** Schematic representation of the body surface of a laboratory rat (from Kaas, 1983). Note that the digits of the forelimb are directed caudally in both bats (C, D), but are directed rostrally in the rat (E).

may appear to be a synapomorphy of bats if they nest within Archonta, but may be interpreted as plesiomorphic if bats fall elsewhere in the mammalian family tree. When homoplasy is evident in a character, the identity of successive sister taxa may greatly influence evolutionary interpretation. If a derived state is present in a clade but absent in at least two successive sister taxa, that condition can be interpreted as a synapomorphy of the clade in question even if the derived state appears in other taxa in the tree. It is not appropriate to reject a putative synapomorphy simply because a similar condition appears in another taxon; the phylogenetic relationships among outgroup taxa must be considered.

Several characters previously cited as chiropteran synapomorphies do not appear to be valid under closer inspection, given the assumptions of this study. Reasons for rejecting each putative synapomorphy are discussed below.

Ramus infraorbitalis of the stapedial artery passes through the cranial cavity dorsal to the alisphenoid. Wible and Novacek (1988) cited an intracranial course of the ramus infraorbitalis of the stapedial artery as a synapomorphy of bats. The majority of eutherian mammals exhibit one of two extracranial courses: passage through the orbitotemporal region ventral to the alisphenoid, or passage through a canal in the alisphenoid (Wible, 1987, 1993; Wible and Novacek, 1988). Based on the distribution of these states, Wible (1987, 1993) and Novacek (1986) argued that passage ventral to the alisphenoid is primitive for Eutheria. In contrast, in bats the ramus infraorbitalis has an intracranial course which passes through the orbitotemporal region dorsal to the alisphenoid (Wible and Novacek, 1988; Wible, 1993). This intracranial vessel is apparently not homologous with the extracranial ramus infraorbitalis of other mammals because both vessels occur in some microchiropterans (Buchanan and Arata, 1967; Wible and Novacek, 1988).

Kallen (1977) indicated that the intracranial ramus infraorbitalis is absent in at least two bat taxa, *Rhinolophus* (Rhinolophidae) and *Desmodus* (Phyllostomidae). Wible and Novacek (1988) interpreted this as a secondarily derived condition because other rhinolophids and phyllostomids possess the intracranial vessel. An intracranial vessel similar to that seen in bats is present in some soricomorph insectivorans, but other soricomorphs and erinaceomorphs lack this vessel (Roux, 1947). This distribution pattern led Wible and Novacek (1988) to conclude that an extracranial ramus infraorbitalis is primitive for insectivorans. Accordingly, the intracranial vessel seen in bats appears to be independently derived, and presence of this vessel was interpreted as a chiropteran synapomorphy by Wible and Novacek (1988).

Recognition of the intracranial ramus infraorbitalis as a synapomorphy of bats assumes that this vessel is absent in the sister taxa of bats. This appeared to be true at the time of Wible and Novacek's (1988) study, but that is no longer the case: Wible (1993) recently noted that an intercranial ramus infraorbitalis is present in juvenile dermopterans. If bats and dermopterans are sister taxa as suggested by Novacek and Wyss (1986), Wible and Novacek (1988), Novacek (1986, 1990, 1992a), Johnson and Kirsch (1993), Szalay and Lucas (1993), Simmons (1993, in prep.), and Wible (1993), then presence of an intracranial ramus infraorbitalis cannot be considered a synapomorphy of bats. Rather, it apparently applies at a higher taxonomic level—that of Volitantia (Dermoptera + Bats).

Lesser tuberosity of humerus projects proximally beyond the level of the articular surface of the humeral head. The lesser tuberosity of the humerus is often called the "trochin" in bats. Beard (1993a) indicated that projection of this structure beyond the level of the articular surface of the humeral head is a synapomorphy of Chiroptera. This condition stands in contrast to that seen in most mammals, where the lesser tuberosity of the humerus does not extend beyond the level of the humeral head (Beard, 1993a; personal obs.).

While projection of the lesser tuberosity beyond the humeral head is clearly derived, Beard's (1993a) interpretation of this feature appears to be incorrect. The lesser tuberosity does *not* extend beyond the articular surface of the humeral head in many microchiropterans (e.g., *Balantiopteryx, Thyroptera, Molossus*; Smith, 1972: fig. 6) nor in any mega-

chiropterans (Vaughan, 1970a: fig. 13; personal obs.). Projection of the lesser tuberosity of the humerus beyond the head appears to be a condition derived within Microchiroptera, and thus cannot be a synapomorphy of bats.

90° rotation of manus. Wible and Novacek (1988: table 3) listed "manus rotated 90° from position typical for quadrupedal mammals" as a synapomorphy of bats. In quadrupedal mammals the axis of flexion of the proximal wrist joint lies roughly parallel to the axis of flexion of the elbow during normal locomotion. This presumably represents the primitive condition for mammals. Morphology of the wrist and elbow in cursorial mammals precludes rotation of the manus, effectively locking the axis of flexion of the manus into the parallel position. In bats, similar modifications of the elbow and reduction of the distal ulna lock the manus into a fixed position relative to the elbow, but the axis of flexion of the proximal wrist joint lies at an angle approximately 90° to that of the elbow. This modification is the result of relative twisting of the distal end of the radius, which has realigned the axis of the radiocarpal facets so that it is perpendicular (rather than parallel) to the axis of flexion of the elbow. While this is clearly a derived condition, it is not unique to bats—dermopterans exhibit the same modifications. If bats and dermopterans are sister taxa, then this derived character cannot be considered a synapomorphy of bats. Rather, it apparently applies at a higher taxonomic level—that of Volitantia.

Absence of pisiform. Beard (1993a) stated that the pisiform is absent in bats, and interpreted this as a synapomorphy of Chiroptera. If the pisiform were absent, this interpretation would be correct; however, the pisiform is present in both microchiropteran and megachiropteran bats (Dobson, 1878; Vaughan, 1959, 1970a; Jepsen, 1966, 1970; Altenbach, 1979; personal obs.). Although concealed in dorsal views of the wrist, a robust, rodlike pisiform extends obliquely across the posteroventral surface of the chiropteran carpus, where it is tightly bound by ligaments to the cuneiform, magnum, and trapezium (Vaughan, 1959, 1970a; Altenbach, 1979: fig. 31; personal obs.). Allen (1893) noted that the pisiform may be absent in pteropines and rhinolophines, but my examination of specimens suggests that the pisiform in these forms is present but may be fused to the magnum. In this context, absence of the pisiform cannot be considered a synapomorphy of bats.

Dorsal ischia meet above vertebral axis. Orientation of the pelvis such that the dorsal ischia meet above the vertebral axis was listed as a possible synapomorphy of bats by Baker et al. (1991b: table 1). While this condition is indeed seen in a few megachiropterans and microchiropterans, my examination of skeletal material indicates that it is not found in the majority of taxa in either suborder. When the derived condition is present (e.g., in *Pteropus*), variation exists even within species. For example, the dorsal ischia meet above the axis of the vertebral column in male *Pteropus tonganus* (e.g., USNM 546349), but not in females of the same species (e.g., USNM 546347). Accordingly, this character does not appear to represent a valid synapomorphy of bats.

Iliosacral fusion involving last lumbar vertebra. Involvement of the last lumbar vertebra in the iliosacral fusion was listed by Baker et al. (1991b: table 1) as a possible synapomorphy of bats. This character is problematic from several perspectives. First, the distinction between "sacral" and "lumbar" vertebrae is typically based on presence/absence of participation in the joint between the ilium and the vertebral column. In evolutionary terms, a vertebra may be transformed from a lumbar to a sacral vertebra by establishment of a joint with the ilium and fusion with the other sacral vertebrae. In some cases it may be recognized as a homolog of the last lumbar vertebrae of other taxa, but such homologies are hard to establish when vertebral counts are taxonomically variable. In bats, the number of thoracic, lumbar, and sacral vertebrae varies considerably among species. For example, Walton and Walton (1970: table 1) noted 11–14 thoracic vertebrae, 4–6 lumbar vertebrae, and 3–6 sacral vertebrae in different bat taxa. Unfortunately, the total number of vertebrae in the thoracic through sacral series also varies among bats (from 19–24; Walton and Walton, 1970), so evolutionary subtraction of vertebrae from one part of the series (e.g., lumbar) does not

necessarily mean that homologs of those vertebrae have been added to another part of the vertebral series (e.g., thoracic or sacral). This makes it very difficult to assess homologies of vertebra associated with the iliosacral fusion.

Even if the character description in Baker et al. (1991b) is interpreted as indicating that the last lumbar can be recognized as such (e.g., it forms a contact with the ilium but is not yet fully fused to the sacral vertebrae), there are still problems with this character. Most importantly, in most megachiropterans and microchiropterans there is no contact between the last lumbar vertebrae (sensu lato) and the ilium. The first vertebra that articulates with the ilium is typically highly modified, with transverse processes that extend the full length of the centrum and contact the ilium along their entire length. The centrum and transverse processes are completely fused with those of the succeeding sacral vertebra, suggesting that the first vertebra involved in the iliosacral joint should be considered a "true" sacral vertebra sensu Flower (1885). In a few instances a case may be made for incorporation of the last lumbar into the iliosacral fusion in a particular specimen, but the evidence supporting this conclusion is based on comparisons of sacral morphology within the species, not among higher taxa. In this context, inclusion of the last lumbar vertebra in the iliosacral fusion does not appear to be a valid synapomorphy of bats.

DISCUSSION AND CONCLUSIONS

The molecular and morphological data currently available strongly support bat monophyly. Although some characters are difficult to interpret, a large number of putative chiropteran synapomorphies have been proposed. For example, 39 derived substitutions in the ϵ-globin sequence, 22 derived substitutions in the IRBP sequence, 8 derived substitutions in the 12S rDNA sequence, and 7 derived substitutions in the COII sequence apparently diagnose Chiroptera (Adkins and Honeycutt, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992; Stanhope et al., 1992, 1993). Over 25 morphological synapomorphies—many of which consist of complex suites of modifications—also diagnose Chiroptera (table 4). The fact that these features represent many different anatomical systems (dentition, skull, cranial vasculature system, postcranial musculoskeletal system, fetal membranes, nervous system) further strengthens the case for bat monophyly.

The degree of character support for Chiroptera compares favorably with perceived support for other mammalian groups that are generally agreed to be monophyletic. Theria, Eutheria, Primates, Carnivora, Perissodactyla, Sirenia, and Proboscidea are each diagnosed by 6–10 morphological synapomorphies, fewer than half the number of features that diagnose Chiroptera (Novacek, 1990; Beard, 1993a; Fischer and Tassy, 1993; Wyss and Flynn, 1993). In the ϵ-globin sequence, over 30 derived substitutions diagnose Chiroptera, while only 4 such substitutions diagnose Primates (Bailey et al., 1992). Alternatively, Primates is diagnosed by 18 transversions in the COII data set, while Chiroptera and Artiodactyla are each diagnosed by 6–7 transversions (Adkins and Honeycutt, 1993). While measurements of branch length clearly depend on taxonomic sampling, tree topology, and methods used to define characters (see discussion below), comparisons of relative character support nevertheless suggest that Chiroptera is one of the better supported clades within Mammalia.

From the conclusion that bats are monophyletic it follows that wings and powered flight evolved only once in mammals. As discussed earlier, the oldest known fossil bats are fully volant microchiropterans from the Early Eocene; megachiropteran bats first appear in the fossil record in the Late Eocene (Jepsen, 1966; Van Valen, 1979; Habersetzer and Storch, 1987; Novacek, 1987; Ducrocq et al., 1993). Given these dates, it seems likely that flight evolved in the chiropteran lineage sometime in the Paleocene or even the Late Cretaceous, 58–70 million years ago. More precise estimates will depend upon increased resolution of the branching pattern of the various eutherian orders.

What is the Sister Group of Bats?

Critical questions remain concerning the place of bats within Eutheria. While most workers now agree that bats are monophy-

TABLE 4
Morphological Synapomorphies of Chiroptera[a]

1) Deciduous dentition does not resemble adult dentition; deciduous teeth with long, sharp, recurved cusps.
2) Palatal process of premaxilla reduced; left and right incisive foramina fused in midsagittal plane.
3) Postpalatine torus absent.
4) Jugal reduced and jugolacrimal contact lost.
5) Two entotympanic elements in the floor of the middle-ear cavity: a large caudal element, and a small rostral element associated with the internal carotid artery.
6) Tegman tympani tapers to an elongate process that projects into the middle-ear cavity medial to the epitympanic recess.
7) Proximal stapedial artery enters cranial cavity medial to the tegmen tympani; ramus inferior passes anteriorly dorsal to the tegmen tympani.
8) Modification of scapula: reorientation of scapular spine and modification of shape of scapular fossae; reduction in height of spine; presence of a well-developed transverse scapular ligament.
9) Modification of elbow: reduction of olecranon process and humeral articular surface on ulna; presence of ulnar patella; absence of olecranon fossa on humerus.
10) Absence of supinator ridge on humerus.
11) Absence of entepicondylar foramen in humerus.
12) Occipitopollicalis muscle and cephalic vein present in leading edge of propatagium.
13) Digits II–V of forelimb elongated with complex carpometacarpal and intermetacarpal joints, support enlarged interdigital flight membranes (patagia); digits III–V lack claws.
14) Modification of hip joint: 90° rotation of hindlimbs effected by reorientation of acetabulum and shaft of femur; neck of femur reduced; ischium tilted dorsolaterally; anterior pubes widely flared and pubic spine present; absence of m. obturator internus.
15) Absence of m. gluteus minimus.
16) Absence of m. sartorius.
17) Vastus muscle complex not differentiated.
18) Modification of ankle joint: reorientation of upper ankle joint facets on calcaneum and astragalus; trochlea of astragalus convex, lacks medial and lateral guiding ridges; tuber of calcaneum projects in plantolateral direction away from ankle and foot; peroneal process absent; sustentacular process of calcaneum reduced, calcaneoastragalar and sustentacular facets on calcaneum and astragalus coalesced; absence of groove on astragalus for tendon of m. flexor digitorum fibularis.
19) Presence of calcar and depressor ossis styliformes muscle.
20) Entocuneiform proximodistally shortened, with flat, triangular distal facet.
21) Elongation of proximal phalanx of digit 1 of foot.
22) Embryonic disc oriented toward tubouterine junction at time of implantation.
23) Differentiation of a free, glandlike yolk sac.
24) Preplacenta and early chorioallantoic placenta diffuse or horseshoe-shaped, with definitive placenta reduced to a more localized discoidal structure.
25) Definitive chorioallantoic placenta endotheliochorial.
26) Cortical somatosensory representation of forelimb reverse of that in other mammals.

[a] See text for discussion.

letic, there is no agreement concerning the identity of the sister taxon of bats. Monophyly of Archonta—a clade supposed to contain bats, dermopterans, primates, scandentians, and several fossil taxa—has been supported by many studies based on morphological data (e.g., Smith and Madkour, 1980; Novacek and Wyss, 1986; Novacek, 1986, 1990, 1992a, in press; Wible and Novacek, 1988; Greenwald, 1991; Johnson and Kirsch, 1993; Szalay and Lucas, 1993) and combined morphological and molecular data (Novacek, 1994). However, archontan monophyly has been rejected in other studies based on analyses of biochemical, molecular, and at least one morphological data set (e.g., Cronin and Sarich, 1980; Miyamoto and Goodman, 1986; Bailey et al., 1992; Kay et al., 1992; Stanhope et al., 1992, 1993; Adkins and Honeycutt, 1993; Honeycutt and Adkins, 1993; Sarich, 1993). Numerous clades of both archontan and non-archontan mammals have been proposed as the sister group of bats (table 5). In this context, it is very difficult to establish just which morphological features (or nucleotide substitutions) are chiropteran synapomorphies. Many unique characteristics of bats, such as morphology of the deciduous dentition, would be considered synapomorphies under any hypothesis

that accepts chiropteran monophyly. However, interpretation of other features varies according to the identity of the sister group of bats.[3]

One source of confusion concerning chiropteran relationships has been uneven taxonomic sampling. Many relevant studies have included only a few taxa, thus groups identified as the sister taxon of bats in some analyses (e.g., Carnivora; Stanhope et al., 1992) were not even considered in other studies (e.g., Adkins and Honeycutt, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992; Kay et al., 1992). Those morphological studies that included data from all or most of the mammalian orders have uniformly identified Dermoptera as the sister group of bats (e.g., Novacek and Wyss, 1986; Novacek, 1986, 1990, 1992; Wible and Novacek, 1988; Greenwald, 1991; Johnson and Kirsch, 1993). In contrast, conclusive molecular studies with comparable taxonomic sampling—all of which have relied on protein amino acid sequence data—have identified the sister taxon of bats as a larger clade including some combination of Scandentia, Insectivora, Carnivora, Pholidota, and Tubulidentata (Miyamoto and Goodman, 1986; Stanhope et al., 1993). Of particular importance is the fact that Dermoptera was *not* included in any of these studies.

Examination of branch lengths in trees based on analyses of molecular data (e.g., Adkins and Honeycutt, 1991, 1993; Stanhope et al., 1992, 1993) and morphology (e.g., Wible and Novacek, 1988; Simmons, 1993) indicates that only a few putative synapomorphies link bats with any other eutherian order. It is clear that Megachiroptera and Microchiroptera share far more synapomorphies with each other than Chiroptera shares with any of its putative sister taxa. How can we account for this pattern, and also for the diversity of opinions concerning the identity of the sister group of bats? Although there are problems associated with any supposition of clocklike evolutionary change (Scherer, 1990), one explanation for the pattern of synapomorphies is that the temporal length of the common ancestral lineage shared by bats and their sister taxon was very short compared to the subsequent period of divergence. Another possibility is that evolution occurred unusually rapidly in the bat lineage subsequent to its separation from its sister lineage. Neither of these hypotheses can be addressed until the relationship of Chiroptera to other mammalian clades has been resolved.

[3] It should be noted that alternative hypotheses of sister-group relationships may increase perceived character support for chiropteran monophyly. For example, in this study I have tentatively accepted Dermoptera as the sister group of bats (see Morphological Characters Supporting Bat Monophyly). Accordingly, derived morphological traits shared by dermopterans and bats have been interpreted as synapomorphies of Volitantia, from which it follows that they must be plesiomorphic for Chiroptera. If Dermoptera and Chiroptera are not sister taxa, however, these features may have evolved independently in the two lineages, and thus may be added to the list of possible synapomorphies of Chiroptera.

Directions for Future Research

Given the compelling evidence which now supports monophyly of Chiroptera, it seems clear that future studies of higher-level relationships of bats should concentrate on resolving the position of bats within Eutheria (and relationships within the two bat suborders) rather than continuing to focus on bat monophyly. While data relevant to bat monophyly will always be of interest, it is time to move beyond this controversy to investigate evolutionary problems at other taxonomic levels.

Future studies directed toward resolving the relationships of Chiroptera to other orders should include several components. Increased taxonomic sampling in the context of some data subsets may prove particularly productive. Analyses of nucleotide sequence data hold great promise, but few studies to date have included representatives of more than half of the extant orders. As demonstrated by Adkins and Honeycutt's (1991, 1993) analyses of COII sequence data, addition of a few taxa can significantly affect the outcome of a study. Future research involving broad sampling of mammalian orders may be expected to reveal phylogenetic patterns not seen in previous studies. However, use of single species as exemplars of diverse orders should be avoided, as artifacts of within-group variation may affect the outcome of analyses of among-group relationships.

TABLE 5
Proposed Sister Group of Chiroptera

Sister clade	Study	Type of data
Dermoptera	Gregory (1910); Novacek and Wyss (1986); Novacek (1986, 1990, 1992a); Wible and Novacek (1988); Greenwald (1991); Johnson and Kirsch (1993); Simmons (1993); Szalay and Lucas (1993); Wible (1993)	Morphological
	Novacek (1994)	Morphological + molecular[a]
Dermoptera + Primates	Beard (1993a, 1993b)	Morphological
Primates + Scandentia	Kay et al. (1992)	Morphological
Dermoptera + Primates + Scandentia[b]	Ammerman and Hillis (1992)	Molecular
Dermoptera + Primates + Scandentia + Lagomorpha[c]	Bailey et al. (1992)	Molecular
Scandentia + Insectivora + Carnivora + Pholidota[d]	Miyamoto and Goodman (1986)	Molecular[e]
Insectivora (excluding *Erinaceus*) + Tubulidentata[d]	Stanhope et al. (1993)	Molecular[f]
Insectivora + Carnivora[d]	Stanhope et al. (1993)	Molecular[g]
Carnivora	Stanhope et al. (1992, 1993)	Molecular[h]
Artiodactyla[i]	Adkins and Honeycutt (1993)	Molecular

[a] The data set included 49 morphological characters and information from 684 base pairs of the COII gene. An analysis including the morphological data plus all substitutions in the COII data could not resolve the sister group of bats. Dermoptera was identified as the sister group in an analysis that included morphological data and COII transversions only.

[b] Archonta was assumed to be monophyletic in the analysis.

[c] The only other taxon included in this study was Artiodactyla, which was used as an outgroup.

[d] Dermoptera was not included in the study.

[e] Combined protein data set including amino acid sequence data from α- and β-globins, myoglobins, lens αA crystallins, fibrinopeptides, cytochrome c, and ribonucleases.

[f] Amino acid sequence data from α - and β-globins.

[g] Combined protein data set including amino acid sequence data from α- and β-globins, myoglobins, lens αA crystallins, fibrinopeptides, cytochrome c, ribonucleases, and embryonic α- and β-globins.

[h] RBP data.

[i] The most parsimonious tree was rooted through an edentate; Carnivora and Insectivora were not included in the study.

When multiple representatives of orders are included in a study, it may be useful to constrain some analyses to preserve ordinal or subordinal monophyly to facilitate investigation of relationships among these groups. Springer and Kirsch (1993) included several artiodactyls, rodents, and bats in their study in order to test monophyly of these orders, but never ran constrained analyses to evaluate eutherian relationships in the context of ordinal monophyly. This omission is unfortunate since there is strong evidence from other data sets that each of these groups is monophyletic (Prothero et al., 1988; Honeycutt and Adkins, 1993; Luckett and Hartenberger, 1993; Simmons, 1993, this paper).

The importance of fossils for understanding higher-level relationships of mammals has

been highlighted in several studies (e.g., Beard, 1990, 1993a; Novacek, 1990, 1992a, 1992b). Although phylogenetic studies including extinct taxa are often plagued by missing data, the information preserved in such taxa may be crucial for understand relationships among extant forms. Studies by Beard (1990, 1993a) and Kay et al. (1992) have demonstrated that extinct paromomyids and plesiadapids should be considered in phylogenetic studies of archontan mammals.

A potentially productive method for resolving bat relationships may be to combine various data subsets in a "total evidence" approach (Kluge, 1989; Jones et al., 1993). Different subsets of morphological characters have been routinely combined in phylogenetic analyses relevant to bat relationships (e.g., Luckett, 1980b, 1993; Smith and Madkour, 1980; Wible and Novacek, 1988; Johnson and Kirsch, 1993; Simmons, 1993), but most molecular studies have focused on only a single gene or protein (e.g., Adkins and Honeycutt, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992). Although some workers have combined different subsets of molecular data (e.g., Czelusniak et al., 1990; Honeycutt and Adkins, 1993), taxonomic sampling has been a problem because different data subsets typically sample significantly different sets of taxa. Only one attempt has been made to combine morphological and molecular character data in a single analysis (i.e., Novacek, 1994).

Studies combining molecular and morphological data are of particular interest when different data sets produce significantly different phylogenies. Although there is some concern that information may be lost when data sets are combined, and that large molecular data sets may "swamp out" the signal from smaller morphological data sets, preliminary results of total evidence analyses have been promising (e.g., Novacek, 1994). Jones et al. (1993: 100) observed recently that

> . . . arguments regarding conflicts between molecular and morphological data are overstated. . . . Rather than increasing uncertainty in phylogenetic inference, we see total evidence as maximizing descriptive and explanatory power. As Moritz and Hillis (1990: 4) pointed out, "studies that incorporate both molecular and morphological data will provide much better descriptions and interpretations of biological diversity than those that focus on just one approach."

Integrated studies that include morphological data from many organ systems—and molecular data from many genes and proteins—may hold the key to unraveling eutherian relationships, including the positions of Chiroptera and Primates. Continuing efforts to identify new character sets, fill sampling gaps, and refine analytical methods should be encouraged in hope that future studies will resolve the persistent problems of mammalian phylogeny.

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